Metapopulation dynamics of Primula vulgaris

Thesis

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Metapopulation Dynamics of *Primula vulgaris*

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To my parents,

with all my love.

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Abstract

Primula vulgaris Huds. shows a patchy distribution within its forest habitat. Each patch is viewed as a local population within a metapopulation. Patches are associated with gaps in the canopy and the foundation and extinction of local populations are coupled with forest canopy dynamics. This study analyses the system formed by local populations and their forest environment with the aim of understanding the factors that affect *P. vulgaris* metapopulation dynamics. Data was collected on the demography of local populations in patches in different light conditions, and on the changes in the canopy brought about by the forest regeneration cycle. These were combined to model the effect of forest disturbance regime and seed dispersal on metapopulation dynamics and overall abundance of *P. vulgaris* in the forest.

The demography of local populations varied spatially in forest patches under different light conditions. Population growth rate (λ) was higher in brighter patches than in closed canopy patches. Population under closed canopy conditions may show negative growth rates which may result in eventual extinction.

The system of forest patches is a dynamic one: canopy gaps are constantly opening and closing. Canopy closure occurs at an exponential rate and the structure of the forest (i.e., proportion of patches with different light conditions) depends largely on the disturbance regime (i.e., rate of gap creation).

Simulation results showed that higher disturbance regimes produced higher metapopulation growth rate and higher overall *P. vulgaris* abundance in the forest. Long-distance seed dispersal reduced overall *P. vulgaris* abundance because it implied an amount of seed loss; however, it increased metapopulation growth rate, as it allowed the colonisation of newly-opened gaps. Under low disturbance regimes, *P. vulgaris* may form non-equilibrium metapopulations. Whether there is a balance between colonisations and extinctions depends on the effectiveness of seed dispersal in allowing the occupation of gaps.

Chapter 1. Introduction

In this chapter I present a general review of various subjects that are relevant in the context of the theme of my thesis. I start by explaining the metapopulation concept, followed by some examples of how the metapopulation theory has been applied for particular plant species. The various links between the metapopulation theory and conservation biology are explained later.

The subject of this study is the metapopulation dynamics of a temperate forest understory herb in which the establishment of local populations occurs after the opening of gaps in the forest canopy. Therefore, the rest of this introductory chapter is dedicated to discuss, first, the effect of canopy gaps on woodland herbs; second, the ecology and demography of woodland herbs; and finally, the role of seed dispersal in linking local populations within metapopulations. At the end of this section the objectives of the thesis are briefly presented.

1.1 The Metapopulation Theory

Conceiving biological systems as dynamic, unstable and changing entities at different temporal and spatial scales has given rise to many important concepts and theories in ecology. As McIntosh (1985, p 69) stated, the key word in the building process of ecology has been *dynamics*. The origin of the metapopulation concept also has its roots in the identification of the dynamic nature of biological systems, in this case, at the scale of groups of populations.

Metapopulations are systems of local populations connected by dispersing individuals. This definition involves the recognition that populations do not work in isolation, but are structured in assemblages or arrays of populations. In this context, local populations are conceived as groups of individuals of the same species occupying a certain area within which most of them are born and die. In a metapopulation, local populations are linked together through migration of individuals between them. The metapopulation concept is, in a way, an abstraction of the population concept to a higher level in which different spatial and temporal scales are considered: at a local scale populations refer to groups of interacting individuals; at a larger scale, metapopulations arise as dynamic systems of such local populations (Hanski and Gilpin 1991).

The dynamics of local population can be described by birth and death rates, and the result of these processes: the rate at which populations increase or decrease in number of individuals. An analogous process occurs at the metapopulation level. However, in this case the units that constitute the group are populations themselves. *Birth* is conceived as the establishment of new populations, while *death* implies population extinction. The analysis of metapopulation dynamics is the study of colonisation and extinction rates and the conditions under which these two processes are in balance (Hanski and Gilpin 1991).

1.1.1 The Origins of the Metapopulation Theory

The word *metapopulation* was coined by Richard Levins in 1970 to describe a population of populations. The development of the metapopulation theory began at the time when the importance of populations as ecological systems had been stated, leading also to the formalisation of ideas concerning their formation and extinction. However, it remained almost untouched by ecologists for more than 20 years, during which population ecology took off and finished its process of consolidation. It was not until the late 80's, when population ecology had produced a substantial amount of information about the functioning of natural populations, that the metapopulation theory reappeared.

By the time Levins proposed the metapopulations concept, the idea of dynamic communities where local colonisations and extinctions were constantly taking place was not a new one in ecology. In 1940 Sewall Wright pointed out the evolutionary and ecological implications of the subdivision of populations into smaller scale units, and later on Andrewartha and Birch (1954) asserted that "a natural population occupying any considerable area will be made up of a number of... local populations", and also considered the importance of colonisations and extinctions under these circumstances.

The theory of island biogeography (MacArthur and Wilson 1967) also referred to colonisation and extinction events and stated their importance in shaping the biological diversity of islands. In this context, Levins explicitly distinguished between the dynamics of single populations and a set of local populations, and introduced new variables to analyse the latter (Hanski and Gilpin 1991).

- Levins' Model

The model proposed by Levins (1969, 1970) is based on several assumptions:

1. The habitat consists of many similar or equivalent patches.

2. The size of populations occupying these patches does not affect metapopulation dynamics. There are only two possible states: presence (at carrying capacity) or absence (extinct).

3. Only colonisation and extinction events are relevant. The local dynamics of populations are ignored.

4. Movement of individuals from occupied patches is equally likely to all other patches. The spatial arrangement of patches has no consequences on the metapopulation and the state of habitat patches (occupied or unoccupied) is not correlated with spatial distribution.

5. The rate of colonisation is proportional to the fraction of occupied patches (p) and to the fraction of unoccupied patches or targets for colonisation ($1-p$).

6. All local populations have the same extinction probability.

Given these assumptions, the rate of change of the occupancy, p, in time is given by

$$\frac{\partial p}{\partial t} = m\,p\,(1\text{-}p) - e\,p \qquad (1)$$

where m and e are the colonisation and extinction rates respectively. At equilibrium, the proportion of patches occupied, p^*, is given by:

$$p^* = 1 - \frac{e}{m} \qquad (\text{or } p^* = \frac{(m\text{-}e)}{m}) \qquad (2)$$

Equation (1) is the model proposed by Levins and provides a simple tool for describing metapopulation dynamics. Equation (2) is fundamentally important in highlighting the key aspect of the model. It summarizes its main predictions: p^* is positive only if $m > e$, that is, a metapopulation may only persist if the rate of establishment of new local populations exceeds the rate of local extinctions (Hanski 1991).

Levins' model has served as the starting point for many theoretical analysis during the last 20 years (Hanski and Gilpin 1991). The main lines of research that have emerged from it are related to a) the causes of extinction - stochastic and deterministic - (Hanski 1991; Harrison 1991; Gotelli 1991; van der Meijden *et al.* 1992; Lande 1993); b) the result of modifying some of the model's assumptions in relation to size and degree of isolation of local populations (Fahrig and Merriam 1985; Fahrig and Paloheimo 1988; Hastings and Wolin 1989); c) the relationship between distribution and abundance - i.e., the core-satellite hypothesis - (Hanski 1982b, 1991; Gotelli 1991; Hanski and Gyllenberg 1993); d) the effect of dispersal on colonisation (Gadgil 1971; Levin 1974; Horvitz and Schemske 1986; Gotelli 1991; Verboom and Lankester 1991; Alvarez-Buylla and García-Barrios 1993; Cipollini *et al.* 1993, 1994 ; Perry and González-Andujar 1993; Overton 1994); and e) the genetic and evolutionary consequences of metapopulation structure and potential isolation between local populations (Slatkin and Wade 1978; Olivieri and Gouyon 1985; Wade and McCauley 1988; Gilpin 1991; McCauley 1991; Lacy 1992).

Recent studies offer empirical basis that support the existence of metapopulations in nature. Most of them have been carried out with animals, such as mice, badgers, birds, toads, butterflies, and other invertebrates (Fahrig and Merriam 1985; Fahrig and Paloheimo 1988; Harrison 1988; Lande 1988; Harrison 1991; Verboom and Lankester 1991; Sinsch 1992; Hanski *et al.* 1994, 1995 among others). Similar research with plant metapopulations has become increasingly important during the last decade, despite the difficulty of estimating seed dispersal between local populations (Holland and Jain 1981; Carter and Prince 1981; Carter and Prince 1988; Hengeveld 1985; Olivieri and Gouyon 1985; Platt and Weiss 1985; Horvitz and Schemske 1986; Gouyon *et al.* 1987; Menges 1990; Alvarez-Buylla and García-Barrios 1991, 1993; van der Meijden *et al.* 1992; Cipollini *et al.* 1993, 1994; Ouborg 1993; Perry and González-Andujar 1993; Overton 1994; Wu and Levin 1994).

1.1.2 Plant Metapopulations

The sub-division of populations in groups or arrays is related to the patchy nature of most natural environments. All populations have a patchy distribution at some scale or another, often reflecting the heterogeneity of the habitat in relation, for instance, to soil composition or spatial patterns of disturbance and recruitment (White and Pickett 1985). The answer to the question of whether individual patches should be regarded as separate populations or as local populations constituting a metapopulation lies in the degree of interrelation between them (Silvertown and Lovett Doust 1993). Metapopulations arise when a significant flow of individuals (seeds in the case of plants) links local populations together, simultaneously allowing for colonisation of unoccupied suitable patches (Levins 1970).

Although the term *metapopulation* has not been used in an explicit manner till recently, the study of related subjects has been widespread in plant ecology. The question of fragmented distributions and patch dynamics has been a permanent field of research in plant ecology and biogeography. The work by Erickson (1943, 1945) is a clear example of this approach. He mapped the spatial distribution of *Clematis fremontii* var. *Riehlii*, a perennial herb that

shows a limited geographical range in Missouri. Within this area, the species is confined to specific suitable habitat patches, and this patchiness can be observed at several spatial scales, from the geographical to the individual level. Suitable patches within the plant's range where found to be empty, perhaps due to extant populations and/or to the inability of seeds to reach and colonise them. Limited seed dispersal between patches at the larger scale probably determines the distribution range of the species. It is likely that other rare taxa also show similar complex patchy distributions (Silvertown and Lovett Doust 1993) in which metapopulation processes, such as colonisations and extinctions, might be playing an important role in defining their distributions limits.

Carter and Prince (1981, 1988) also addressed the subject of distribution limits with interesting results. They observed that many species show rather sharp geographical distribution limits apparently unrelated to equivalent changes in environmental conditions. Geographical and topographical trends in environmental conditions are often less abrupt than plant distribution limits. Although populations do not establish beyond these boundaries, individual plants seem to be able to survive, grow, and reproduce out of the species' distribution range (Levin and Clay 1984). Carter and Prince (1988) studied the distribution of *Lactuca serriola* and suggested that small changes in climatic factors may produce slight differences in the demography of populations, which in turn can alter the balance between extinction and colonisation at the metapopulation level. Only very slight changes in extinction or colonisation rates may be sufficient to cross the threshold from a situation in which the metapopulation would be spreading to a condition in which it would be unsustainable. Thus, the cause of distribution limits for some species might be explained by metapopulation dynamics, and not by the performance of individual plants or populations.

From this perspective, the spreading of plant species through the invasion of new geographical areas can be explained as a metapopulation phenomenon as well. Spreading species are growing metapopulations in which the rate of population foundation exceeds the

rate of extinction. Carter and Prince (1981) showed that this process can be understood through a model identical in form to the general deterministic epidemic model, which is central to the theory of infectious diseases. In this model colonisable patches are analogous to susceptible sites, while colonisation is equivalent to infection and dispersal corresponds to the dissemination process.

Host-parasite relationships are thus a good example of the functioning of metapopulations. In fact, Overton (1994) applied a metapopulation model to explain the role of seed dispersal patterns on the local distribution and abundance of a parasite plant, the mistletoe *Phrygilanthus sonorae*, that infects *Bursera* trees in the Sonoran desert. He showed that the recognition of the spatial structure of mistletoe populations as a metapopulation was essential in explaining the observed patterns of infection, which were strongly related to the observed patterns of seeds dispersal by birds.

It has been suggested that metapopulation processes (e.g., long-distance seed dispersal and colonisation) have also been important in the geographic spread of some species in geological time: invasions appear to have occurred through the foundation of populations beyond the species' original boundaries (Bossema 1979; Davis *et al.* 1994). The patterns and rates of spread of oak in Britain (Skellam 1951) and of oak and beech in North America (Johnson and Webb 1989) - obtained through fossil pollen maps - show that they have been far too fast for them to have happened along an advancing front. A model including colinisation through long-distance dispersal is needed to explain such invasion patterns.

Recent research has demonstrated that the evidence for the existence of metapopulations in plants go beyond the recognition of spatially structured populations. Ouborg (1993) showed that the colonisation of unoccupied patches by *Erygnium campestre*, *Medicago falcata* and *Plantago media* along the Rhine-system in Holland does not occur at random; both colonisation and extinction are influenced by isolation from other occupied patches, which strongly suggests that these species have metapopulation structures. Other studies

have directly addressed the functioning of plant metapopulations of various kind of species from different habitat types, with results that point towards the consolidation of the metapopulation concept in plant ecology (Platt and Weiss 1985; Horvitz and Schemske 1986; Menges 1990; Alvarez-Buylla and García-Barrios 1991; Lesica 1992; van der Meijden *et al.* 1992; Cipollini *et al.* 1993, 1994; Overton 1994).

1.1.3 Metapopulations and Conservation

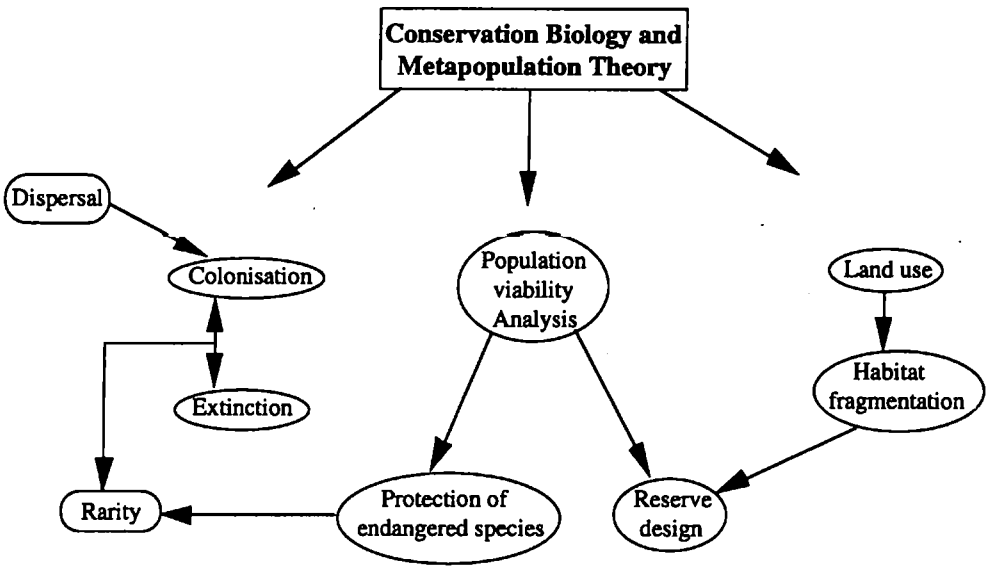
The metapopulation theory has re-appeared in ecology especially during the last decade, also when the impact of conservation biology became more ubiquitous in ecology. Since then, it has provided a natural framework for considering a number of issues relevant to the preservation of species and ecosystems (Hanski 1989).

Several aspects of conservation biology are related in different ways to the metapopulation theory (Fig. 1.1). Extinction itself is a major subject of concern in conservation, and perhaps one of the reasons why the metapopulation theory has served as a link between ecology and conservation lies on the fact that the issue has been addressed in a direct and specific manner, offering answers to an otherwise unexplored field of research. The theoretical considerations arising from the understanding of extinction and colonisations had also offered an insight into the causes of rarity, by examining the different aspects that limit the distribution and abundance of rare species. Most endangered plants are rare species that occur in rather restricted habitats and/or in extremely low numbers (Rabinowitz 1981; Fiedler and Ahouse 1992; Lesica 1992).

Population viability analysis has been an important tool in the study of endangered species (Soulé 1987). It was designed to estimate minimum viable populations - "minimum population size below which the combined effects of random genetic changes and demographic variation would likely result in extinction" (Lacy 1992). Together with other demographic studies oriented towards the conservation of rare species, it has concentrated

on particular local populations (Harvey 1985; Menges 1990). However, this may be misleading if species are spatially structured and rarity is related to metapopulation processes (Silvertown and Lovett Doust 1993).

Figure 1.1 Various links between metapopulation theory and conservation biology.



Metapopulation theory has also an important role in reserve design. Until recently the theory of island biogeography (MacArthur and Wilson 1967) was considered as the theory for reserve design providing arguments about how best to allocate a certain total area to one large or many small reserves (Hanski 1989). The spatial scale at which the metapopulations of particular endangered species are structured could offer an additional element to consider in this controversy (Lande 1988; Lesica 1992).

Finally, many species with an original continuous spatial distribution are being forced into metapopulation structures by habitat fragmentation (Harris and Silva-López 1992; Hanski *et al.* 1994). The dynamics of such fragmented populations has to be understood in order to apply management remedies that would prevent total extinction of such species (Hanski and Gilpin 1991).

Susan Harrison (1994) has questioned the usefulness of the metapopulation theory ("it can produce neither powerful generalizations, nor ready-to-use formulas") on the grounds of the non-existence of real strict metapopulations in nature that meet the assumptions described by Levins (1969, 1970), mainly because local populations may or may not be interconnected or go extinct. The practical use of the metapopulation theory to solve particular conservation problems and also as a conceptual and theoretical tool, though, is that it provides us with a means of relating population dynamics to the structure of the environment, and the size and isolation of habitat patches (Hanski 1989). As with other general models, its value is *strategic* (*sensu* May 1974), giving insight into processes rather than making accurate predictions (Carter and Prince 1988).

1.2 Forest Gaps and Woodland Understory Herbs

This section is devoted to some general aspects of the ecology and demography of temperate woodland herbs and the way in which they are affected by the dynamics of the forest canopy.

1.2.1 Canopy Dynamics

Disturbances in natural communities produce spatio-temporal heterogeneity and patch effects. Natural disturbances and patch dynamics occur on a wide variety of spatial and temporal scales, and thus, the particular definition of patch will always be relative to the system in question (White and Pickett 1985). Small natural disturbances at the level of the forest canopy , such as branch or tree falls, produce the opening of gaps. These eventually close due to the growth of adjacent vegetation and the replacement of new canopy individuals (Runkle 1981; Runkle and Yetter 1987). The permanent process of opening and closure of gaps in the forest canopy is a source of environmental heterogeneity, creating a

mosaic of regenerating phases represented by patches of various sizes and ages (Brokaw 1985b; Martínez-Ramos *et al.* 1988).

A parameter that has proved useful in summarising information on the regeneration dynamics of a forest is the *disturbance regime*, i.e., the pattern of death of dominant individuals in the community (Runkle 1985). The disturbance regime is the rate at which new disturbances occur, and can be measured as the proportion of the area of a forest that is affected by disturbances every given period of time. Another important variable, the *turnover rate*, is defined as the mean time between successive gap formation at any one point in the forest (Brokaw 1985b).

If disturbance regimes are too high, then the establishment of a tree-based community is no longer possible. Thus, natural disturbance regimes for forests have theoretical minimum values set by the maximum age and size limits of tree species (Runkle 1985). Disturbance regimes for temperate forests show surprisingly little variation, despite wide differences in vegetation types and kind of disturbances involved. They are around 1% of the area per year (ranging from 0.5% to 2.0%, which gives natural turnover rates of 50 to 200 years - (Runkle 1985). Very similar values have been obtained for other type of woodland areas, such as tropical and subalpine forest (Brokaw 1985b; Veblen *et al.* 1994).

The rate at which gaps close depends, among other things, on the characteristics of the gap, such as its size and shape. Small gaps usually close through the lateral extension of branches of bordering canopy trees. Average rates of lateral extension of bordering trees range from 4 to 14 cm per year, and some trees can expand at rates of 20 to 26 cm per year (Runkle 1982), or even as fast as 35 cm per year (Cipollini *et al.* 1993).

On the other hand, the closure of big gaps depends mainly upon the growth of individual trees into the canopy (Runkle 1981; Merrens and Peart 1992). However, the rate of sapling height growth of some tree species is quite slow and Runkle (1984, 1985) has suggested

that multiple-gap episodes must be important in allowing them to reach canopy height. The maximum time needed for a gap to close is given by the time required by new saplings to reach a 10-20 m height combined with the effect of the lateral extension of adjacent trees. According to the ranges of sapling height growth that have been reported for various studies in deciduous forests, Runkle (1982) estimated that possible maximum gap ages must be between 10 and 40 years.

1.2.2 The Effect of Canopy Gaps on Woodland Herbs

The gap-phase of the forest canopy regeneration cycle is important in determining the floristic composition of a forest because it allows the establishment and growth of canopy and understory vegetation, thus contributing to the maintenance of community diversity (Denslow 1987; Whitmore 1988, 1989; Barkham 1992a). Following disturbance there is usually an increase of temperature, light, water and nutrients formerly being captured by the pre-disturbance vegetation. The decay of the organic matter released after disturbance (the fallen tree, for instance) brings a further nutrient pulse to the vegetation in the gap. These conditions favour the establishment of understory vegetation and pioneer and canopy tree species, as well as the growth of saplings already present in the site (Brokaw 1985a; Collins *et al.* 1985).

Many understory herbs in a forest depend to a certain extent on gap formation for the accomplishment of one or several phases of their life cycle. The relative temperature increment that occurs in gaps, for instance, can affect different aspects of plant phenology. Flower production, germination and growth of some woodland herbs is enhanced with the relative temperature increment or with the large temperature fluctuations characteristic of gaps (Collins *et al.* 1985).

Herbs can be grouped in three major categories in relation to their photosynthetic response: sun plants, shade plants and light-flexible species (Collins *et al.* 1985). Most woodland

herbs can be classified either as shade plants or as light flexible species. Shade plants develop under closed canopy conditions and an increase in solar radiation is detrimental. Whigham (1974) observed that flowering and vegetative spreading were lower under brighter conditions for the shade plant, *Uvularia perfoliata* (Whigham 1974). However, some light-flexible species prefer gap conditions rather than closed canopy, despite being shade tolerant to a great extent. Barkham (1980) found that vegetative growth and the probability of flowering of *Narcissus pseudonarcissus* were higher in open sites than under the canopy and seed production was also enhanced in brighter conditions. The reproductive output in *Cynoglossum virginianum* plants growing in gap conditions is higher when compared to those growing in the shade (Cipollini *et al.* 1993). Kennedy and Swaine (1992), working on gap-colonising species in a dipterocarp forest, found that seedling growth is enhanced and mortality is reduced when light availability increases.

Although the increase in soil moisture and nutrient availability following disturbance has been widely documented, very little is know regarding the response of woodland herbs to these environmental changes. A high internal concentration of nutrients has been observed in some gap-colonising herb species such as *Hyacinthoides non-scripta* or *Erythronium americanum* (Collins *et al.* 1985); this could be the result of both greater light intensity and higher soil nutrient concentration present in gaps.

Finally, regarding water relations, Elias (1978, 1981, cited in Collins *et al.* 1985) found that water-holding capacity of some temperate forest herbs was low and that they lost water quickly under desiccation due to high maximal transpiration rates. This suggests that these herbs benefit from the relatively high soil water content that prevails in clearings. However, Collins *et al.* (1985) indicate that herbs vary widely in assimilation, growth, and allocation patterns in response to fluctuation in soil moisture.

1.2.3 Ecology and Demography of Woodland Herbs

- General Ecological Features

Most woodland herbs are perennials with relatively long life spans. *Narcissus pseudonarcissus* genets can live from 12 to 18 years (Barkham 1980), *Erythronium japonicum* more than 20 years (Kawano *et al.* 1987), and *Arisaema triphyllum* between 15 and 25 years (Bierzychudek 1982b). The age of first reproduction ranges from 2 or 3 years (for *Primula vulgaris* - Boyd 1986 - and *Uvularia perfoliata* - Whigham 1974 - respectively) to 9 years in *Allium victorialis* (Kawano *et al.* 1987). Annuals are relatively rare and when they occur in woodland habitats they are light-demanding species that grow in gaps and forest edges.

Many deciduous forest herbs can spread vegetatively as well as by seed. In some of them the establishment of new individuals from seed is uncommon once high densities are reached after initial colonisation, and most replacement of individuals is done by vegetative spread. Such is the case of *Clintonia borealis* (Pitelka *et al.* 1985), *Paris tetraphylla* (Hara and Wakahara 1994), *Narcissus pseudonarcissus* (Barkham 1980, 1992b) and *Erythronium americanum* (Kawano *et al.* 1987). However, polycarpic perennials that do not spread vegetatively, and thus, rely only on seeds to maintain their populations are also frequent in this habitat (Bierzychudek 1982b).

Frequently, seeds of temperate forest herbs need to undergo a cold period to germinate and are enhanced by light to do so; only a few have dormancy periods longer than 6 months. Mortality during the seedling phase is extremely high, as seems to be true for plants in general (Harper 1977; Bierzychudek 1982b). The probability of death is usually size-dependent (Cook 1980), and thus, rates of adult mortality are quite low, which is the basis for the long life-spans estimated for these species (Bierzychudek 1982b).

The pollination syndromes observed among forest herbs are varied. A few species are wind-pollinated, but insect-pollinated plants are the most common. Pollination success is thus frequently determined by the availability of pollinators, which in some cases explains the low seed numbers observed in some species (Bierzychudek 1982b; Calvo and Horvitz 1990). Pollination success can be as low as 5%, as shown for *Maianthemum bifolium* and *M. dilatatum* (Kawano *et al.* 1968). However, there is little information about pollen dispersal distances and the genetic structure of populations is mostly unknown.

Many deciduous forest herbs do not posses any special seed dispersal mechanisms. Often seeds just mature and fall off the stem and so they remain within a short distance from the parent plant. Some common seed dispersal vectors in this group of plants include ants (elaiosome-bearing seeds) or birds and mammals (fleshy fruits or seeds with hooks or hair) (Bierzychudek 1982b).

- Population Dynamics and Demography

The tendency in plant demography has been to classify individuals by size or stage, because some demographic parameters such as mortality and fecundity are more dependent on plant size than on age (Werner and Caswell 1977; Caswell 1989). A few comparative studies have indicated that forest herbs usually exhibit population structures in which plants at initial stages or smaller sizes (such as seeds and seedlings) are relatively more frequent than larger ones, with each succeeding class containing even fewer individuals. This is a result of mortality being size-related, with smaller plants being more vulnerable. As a large fraction of the population belongs to the smallest size classes, there is generally a low proportion of reproductive individuals (Bierzychudek 1982b; Kawano *et al.* 1987).

Most recent demographic studies on forest herbs have adapted the population matrix technique of Lefkovitch (Lefkovitch 1965) to the life cycle of stage or size classified plant populations. This technique applies a matrix model to calculate the finite rate of increase, λ,

the stable stage distribution, and the stage-specific reproductive values for populations with complex life cycles.

The basic matrix model is given by

$$\mathbf{n}_{(t+1)} = \mathbf{A}\,\mathbf{n}_{(t)} \qquad (3)$$

where **n** is a vector of nx1 dimensions whose elements, a_{i1}, are the number of individuals that belong to the *i*-th category at time t; **A** is a non-negative square matrix of dimensions nxn, whose elements, a_{ij}, are the transitions or contributions from individuals in the *j*-th category to individuals in the *i*-th category in one time step. These are given by the survivorship, growth and fecundity of the population between t and t+1. Some of the mathematical properties of the matrix correspond to specific demographic parameters of the population. The dominant eigen-value of the matrix is the finite rate of increase, λ, which may be interpreted as a measure of the average fitness of the population; the right dominant eigen-vector is the stable-size or stage distribution, and the left eigen-vector corresponds to the size- or stage-specific reproductive values (Caswell 1989).

Derived directly from population projection matrices, sensitivity and elasticity analysis have provided a powerful tool to study the importance of different phases of the life cycle for population growth. Sensitivity analysis measures the impact on λ of a small change in the individual transitions of the matrix **A**, a_{ij}, relative to changes of the same magnitude in other elements of **A** (de Kroon *et al.* 1986). An analytical measure of proportional sensitivity is given by the elasticity, which measures the proportional contribution of each matrix element, a_{ij}, to λ. The sum of all the elasticities of a matrix equals unity, which allows for comparisons of the demography of different species or populations of the same species (de Kroon *et al.* 1986; Caswell 1989).

The study of the demography of forest herbs has been a matter of increasing interest among ecologists in the past two decades and the question arises as to whether the results

obtained so far suggest any demographic trends or patterns among them. In a comparative demographic study, Silvertown *et al.* (1993) analysed the projection and the elasticity matrices of 14 forest perennial herbs from tropical and temperate habitats and found that the λ of most of these species is close to unity, with most values ranging from 0.97 to 1.16 (the highest values being 1.59 for *Allium monanthum*, and the lowest 0.94 for *Disporum sessile* - Kawano *et al.* 1987). Even though these data suggest that forest herb populations are fairly stable, it has been shown that many populations behave quite differently from year to year and fluctuations in population size seem to be more the rule than the exception (Barkham 1980; Bierzychudek 1982b; Horvitz and Schemske 1995).

The relative contribution of different entries of the matrices to λ, as measured by the elasticity, showed some interesting trends amongst forest herbs. In general, elasticity values for the earliest transitions (seed to seedling) and for the fecundity elements were low. In 11 species out of 14 the elasticity for recruitment of seeds to the seed pool was zero and most values for the recruitment of seedlings ranged between 0.0003 in *Allium monanthum* to 0.0859 for *Calochortus pulchellus*, with the only two extreme cases cases being 0.2659 for *Calathea ovandensis* and zero for *Clintonia borealis*, in which no recruitment from seed was observed (Silvertown *et al.* 1993).

The highest elasticities were found in most cases in the elements of the matrix that implied either stasis or transition to the following size or stage categories. The larger value for stasis was 0.785 for *Narcissus pseudonarcissus*, and for progression to following categories was 0.563 for *Arisaema serratum* (Silvertown *et al.* 1993). These results suggest that the population growth rate of most forest herb populations is strongly dependent on adult survival and growth.

1.3 The Role of Dispersal in Metapopulations

As pointed out before, most populations have a patchy distribution at one scale or another. Whether a set of patches or local populations constitute a metapopulation depends on the degree of interconnection between patches, that is, on how much the dynamics of the whole system is determined by dispersal of individuals between patches. The metapopulation character of a group of local populations is determined to a great extent by the effect of dispersal in the colonisation-extinction balance.

The degree of connectivity between plant populations is not obvious in most cases, which has created some debate about the applicability of the metapopulation concept to plants (Silvertown 1991). However, it has been shown that patchy distributions in plants are evident at a scale at which dispersal could potentially play a major role in connecting populations together. While habitat heterogeneity often occurs on various spatial and temporal scales, there are scales on which patches are fundamental to the structure and functioning of the system in question (Wu and Levin 1994).

This consideration of scale is also sensible regarding seed dispersal: it takes place at several scales but it is relevant to metapopulation dynamics only if it occurs at the scale at which colonisable patches occur in the environment. In this sense, the study of environmental patch dynamics together with the analysis of the seed shadows of particular species is of major interest to metapopulation ecology (Silvertown 1991).

Willson (1993) analysed much information on seed shadows of a large number of species (around 80). The shape of the seed shadow of roughly 85% of them conforms to a negative exponential: the number of seeds dispersed away from the parent plant decreases exponentially as distance increases. A large part of the seeds are deposited close to the source, though a fraction of them can travel longer distances. The scale at which this

happens depends, among other things, on the dispersal agents involved. Yet a distinction can be made for most spatially structured populations between the seeds that remain within the limits of the patch occupied by the population (short-distance seed dispersal) and the seeds that are dispersed beyond its boundaries (long-distance seed dispersal).

Long-distance dispersal represents a cost from several points of view. Dispersal represents a high mortality risk due to the decreased probability of encountering a safe-site for germination, and also as a result of 'handling' by dispersal vectors. Additionally, plants have to face the energy allocation cost of dispersal structures such as eliosomes, fruit pulp, hooks, or wings (Venable and Brown 1993).

If long-distance dispersal has evolved despite its inherent costs, then it must offer some advantages as well. Most of its positive effects could be stated in three general (but not mutually exclusive) hypotheses: 1) that seed dispersal reduces density-dependent seed and seedling mortality near the parent; 2) that seed dispersal may result in non-random movement of seeds towards safe sites; and 3) that dispersal may allow plants to colonise ephemeral patches away from the original population (Murray 1986).

From the metapopulation dynamics point of view, the third hypothesis seems most relevant. Long-distance dispersal involves the probability of encountering unoccupied colonisable patches, which determines the survival and persistence of the metapopulation itself. The theoretical value of this particular aspect of long-distance seed dispersal has been stated by several studies. In a model developed by Venable and Brown (1993), it was shown that dispersal could have evolved as a means of reducing risk only if global (metapopulation) temporal variance was included. Perry and González-Andujar (1993) modeled the behaviour of an hypothetical annual plant and found that dispersal aided metapopulation growth in a spatially heterogeneous environment. Furthermore, Murray (1986) showed that reproductive success was higher when more extensive seed dispersal occurred, mainly for those species that required small gaps to germinate and establish.

The importance of long-distance seed dispersal has been unquestionable when analysed in terms of metapopulation dynamics, not only in purely theoretical models but also when applied to real biological systems. For instance, increased long-distance seed dispersal had a positive effect on population growth rate of a forest shrub (*Lindera benzoin*) and of an understory herb (*Cynoglossum virginianum*) in two metapopulation studies carried out by Cipollini *et al.* (1993, 1994); the primary factor influencing the behaviour of the metapopulation of a moss species that establishes in rotting wood (*Orthodontium lineare*) was spore transport (Herben *et al.* 1991); and finally, the distribution pattern of the mistletoe *Phrygilanthus sonorae* on *Bursera* trees in different sites at the Sonoran desert was explained by the patterns of long-distance (off-tree) seed dispersal by birds (Overton 1994).

1.4 Objectives

Primula vulgaris Huds. is a common element of the ground flora of temperate woodlands in Britain. It shows a spatially heterogeneous distribution within the forests where it occurs, often inhabiting dense patches with sharp boundaries. The main factor that explains this distribution pattern is that populations are associated with the opening of gaps in the forest canopy which allows their establishment and growth.

Within a forest one can find a number of *P. vulgaris* patches apparently functioning as rather independent units. My thesis is based on the hypothesis that these patches are local populations grouped together in metapopulations. When a gap opens in the canopy, *P. vulgaris* seeds may germinate in it and a population is founded. After some time the gap closes and eventually a full canopy cover develops, which may result in population decay and possibly extinction. The metapopulation as a whole, formed by a number of interacting local populations, is seen as a dynamic system in which colonisations and extinctions are constantly occurring. Colonisations are affected by the rate of gap opening in the canopy

and the dispersal of seed to such sites, and extinctions are affected by the rate of canopy closure. In this sense, *P. vulgaris* metapopulation dynamics is coupled with forest canopy dynamics.

The general objectives of my theses are:

1) To build a model to describe the dynamics of a metapopulation of *P. vulgaris* using empirical data on

a) the demography of local populations and

b) forest canopy dynamics.

2) To use the model to test the dependence of metapopulation growth rate on different ecological processes, in particular

a) long-distance seed dispersal and

b) the rate of canopy gap formation.

Chapter 2 presents a description of the species studied and the sites in which the field work was carried out. In order to describe the metapopulation dynamics of *P. vulgaris*, two different scales were examined: the dynamics of local populations within the forest and the dynamics of the forest canopy as a whole. Chapter 3 presents the main results of the demographic analysis of several local populations of *P. vulgaris* in different forest patches along a light gradient. Chapter 4 considers the larger-scale process of canopy dynamics, analysing the rates of canopy closure from hemispherical photographs, as well as the structure of the forest in terms of the relative frequency of patches in different stages along the canopy regeneration cycle.

Chapter 5 combines the information of the two previous chapters in a matrix model that considers both the dynamics of local populations in different forest patches, and the fact that those patches change in time as canopy closure proceeds. This model describes the dynamics of the overall population of *P. vulgaris* in the forest as a whole (in terms of the change in the *number of individuals*), and serves as a basis to explore the effect of seed

dispersal and canopy disturbance regime on overall population growth rate. In contrast, chapter 6 addresses a different spatial scale and focuses on the changes *in the number of local populations* in the forest. It presents a metapopulation dynamics model that includes 1) the transitions of local populations among different stages as the canopy closes, 2) local population extinction probability, and 3) the foundation of populations through the colonisation of newly-opened gaps. These parameters are used to build a metapopulation projection matrix and to test the effect of different levels of seed dispersal and disturbance regime on metapopulation growth rate. Finally, the general discussion in chapter 7 evaluates the main contributions of the results.

Chapter 2. Species and Study sites

2.1 The species studied: *Primula vulgaris* Huds.

2.1.1. Life History and Phenology

The common primrose belongs to the family Primulaceae. It is a perennial herb characteristic of moist shaded habitats in Britain and northern Europe. It is typically a plant of rather open deciduous woodland on soils ranging from heavy and slightly acidic to limy. It seldom grows in full sun or very open habitats, and is not favoured by peaty soils, very light and acidic soils or heavily waterlogged areas (Richards 1989, 1993).

It produces oval, wrinkled, leaves in one or several basal rosettes (Figure 2.1). Vegetative spread occurs within short distances through the production of new rosettes. In Britain, mature plants generally loose old leaves during the autumn. Production of new leaves occurs in late winter, immediately followed by flowering that starts in late February or the beginning of March. Flowers are distylous (see below), pale yellow, usually with diffuse orange markings in the centre, and are born in separate stalks.

The peak of the flowering period is in April and capsules ripe and open around the middle of June, when seed dispersal takes place. Seeds are dark brown, irregularly shaped, about 1.5 mm in diameter. They have a fatty body in the outside called the elaiosome which is attractive to ants, which pick up seeds directly from the capsule and carry them to their nests

(Keith-Lucas 1968; Richards 1989). Seeds are also removed by rodents and other small mammals to which ripe capsules represent an attractive harvest.

Figure 2.1 *Primula vulgaris*, the common primrose (photograph by Mike Dodd).

According to its patchy distribution, the seed dispersal pattern in nature appears to be 'clumped', rather than random (Richards 1989). However, direct observations indicate that seeds generally disperse within short distances. Keith-Lucas (1968) observed seeds being dispersed by ants close to parent plants; in a neighbourhood size study Cahalan and Gliddon (1985) reported that, in the absence of ant dispersal, most seeds landed a few centimetres away from the parent plant.

Seeds germinate in the field during early spring. However, high percentages of seed germination have been observed in controlled conditions with recently collected seeds, indicating that they do not require a cold period and that germination could take place in the field immediately after dispersal. Helliwell (1980) found that germination is enhanced by light and that seeds lose viability after nine months of dry storage.

The juvenile phase can be prolonged, depending on microsite conditions, as plants must grow to a minimum size before reaching sexual maturity. Most plants reproduce for the first time two years after germination, though some can take longer and a few can flower on their first year (Boyd *et al.* 1990). According to the estimates of Mark Boyd *et al.* (1990), plants can live for 10 to 30 years, though no direct observations on longevity are presently available for this species.

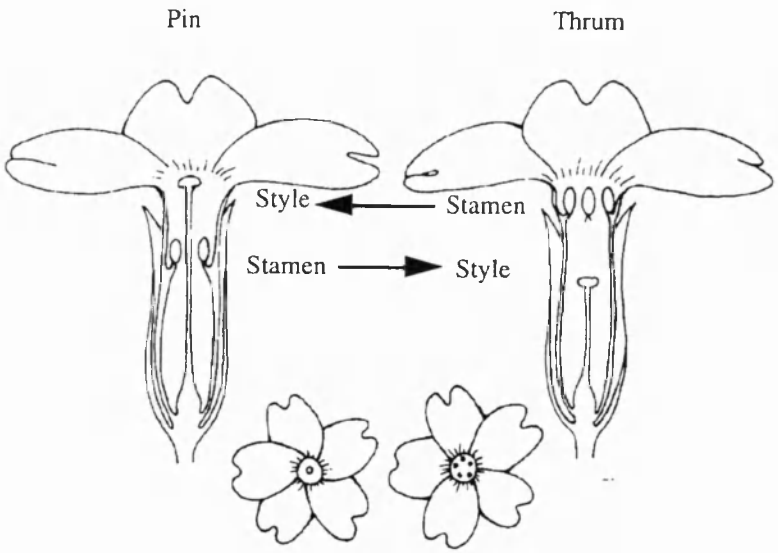
2.1.2 Reproductive Biology

P. vulgaris flowers present a tubular corolla that ends in five spreading yellow petals. Like most members of the genus, it is a distylous species. In most populations two heterostyle flower morphs can be found: pin and thrum. The pin form has the stigma extending to the top of the corolla tube and the anthers near the middle of the corolla tube, while in the thrum morph the position of stigma and anthers is reversed (Figure 2.2).

Distyly represents an incompatibility system that, in fact, restricts legitimate pollination to that between pin and thrum flower morphs. This restriction is not purely morphological. Thrums are totally self-sterile. However, some degree of self-fertility is possible among pins (Richards 1993, p 56).

A third morph can be found in some areas of the West Country, which combines the long anthers of the thrum morph with the long stigma of the pin morph. Thus, in this self-fertile 'homostyle' the anthers and stigma are at the same height near the top of the corolla tube.

Figure 2.2 Pin and thrum flower morphs in *P. vulgaris* (from Silvertown and Lovett Doust 1993).



Heterostyly is determined by a supergene complex which comprises the two alleles, *S* and *s*. The dominant allele *S* produces the thrum morph, while the pin morph is given by the recessive homozygote, *ss*. In most populations only the heterostyle *Ss* and the recessive homostyle *ss* are present, giving rise to thrum and pin morphs respectively. Crossed-pollination results in the progeny of any particular plant being half pin and half thrum.

The homostyle is produced by a third allele, *s'* which is dominant to *s* and recessive to *S* . Homostyle pollen can fertilize pin (*ss*) flowers, all of whose seeds will be homostyle if the pollen is homozigote (*s's'*). Only half the progeny of a pin flower will be homostyle if the pollen comes from an heterozygote homostyle (*s's*).

Despite the advantage of homostyles of being self-fertile and, therefore, not depending on the availability of pollinators to produce seeds, their occurrence in wild populations is less than 1% (Richards 1993). Homostyles have remained localized and rare and several explanations have been offered regarding their low occurrence. Richards (1984) believes that predation by slugs and snails, that graze the tops of primrose flowers, could determine the functioning of pins as male flowers and thrums as female flowers, while seed set by

homostyles would be totally inhibited by predation. Boyd *et al.* (1990) investigated other ecological reasons for the low frequency of homostyles in nature and found that they tend to produce a larger number of seeds when compared with heterostyles, with the consequence that seeds are smaller in size. This could decrease the survival probabilities of homostyle seedlings.

Seed set in the heterostyle morphs is pollinator-limited. Pollinator abundance thus possibly accounts for the wide yearly variation in seed production observed in primrose populations (Piper *et al.* 1984). Flowers are visited by a wide range of long-tongued insects such as hoverflies, bee-flies, bumble-bees, butterflies and moths (Richards 1989). However, there has been a long debate about which species effectively pollinate *P. vulgaris* flowers, as its early flowering does not coincide with the peak activity of pollinators and few insects have been seen actually carrying primrose pollen (Dallman 1921; Woodell 1960). Several studies have conclude that moths must play an important role in primrose pollination since a number of moth species are also present at the time of flower production and flower features correspond to those that would attract night-flying insects (Dallman 1921; Boyd *et al.* 1990).

2.1.3 Geographic Distribution

P. vulgaris grows in habitats which are cool and humid in summer and relatively mild in winter. Therefore, its distribution is largely Atlantic and Mediterranean (Valentine 1948; Richards 1993). It is common in western and southern Europe and abundant in many places in Britain.

It is found in southern Norway and Sweden, Denmark, the British Isles, France, northern and western Iberia, Italy, Greece, the area that corresponds to former Yugoslavia, south-west and northern Turkey, south-west Ukrania, the Crimea and Caucasus and southern shores of the Caspian sea. It is present in most of the larger Mediterranean islands, though

absent from Sardinia and Cyprus. It is also common in North Africa from Gibraltar to Tunisia, as well as in Lebanon, Syria and Israel (Richards 1993).

Within the British Isles, the primrose is recorded in all vice-counties and is common in many places. It is found in a wide range of soil types and its distribution at a more local scale appears to be correlated with soil moisture and atmospheric humidity. In the central region of East Anglia it is mainly found in woodlands, while in the west of England, where precipitation and humidity are higher than in East Anglia, it is common in more open habitats (Valentine 1948).

2.2 The study sites

Most of the field work was conducted at Dancers End Nature Reserve, though *P. vulgaris* populations in two other forests were also studied. A brief description of the three areas is given in the following sections.

2.2.1 Dancers End

Dancers End Nature Reserve is part of a complex of protected areas, currently managed by BBONT, that altogether (with The Crong Meadow and Dancers End Waterworks) cover 37 hectares (92.2 acres) in Buckinghamshire. It lies just south-west of Tring and near Wendover on the Chiltern Hills escarpment (Grid Reference SP 902 096). Its location, geology and past land use make it an area of particularly high floristic richness, with 295 vascular plants having been recorded (MSC Management Plan Team, 1988). In fact, it forms part of a larger Dancers End SSSI area recognised by English Nature.

The majority of the reserve is covered by woodland of various types. Much of Round Spring Wood and Bittam's Wood (Fig. 2.3) were clear felled between 1942 and 1944.

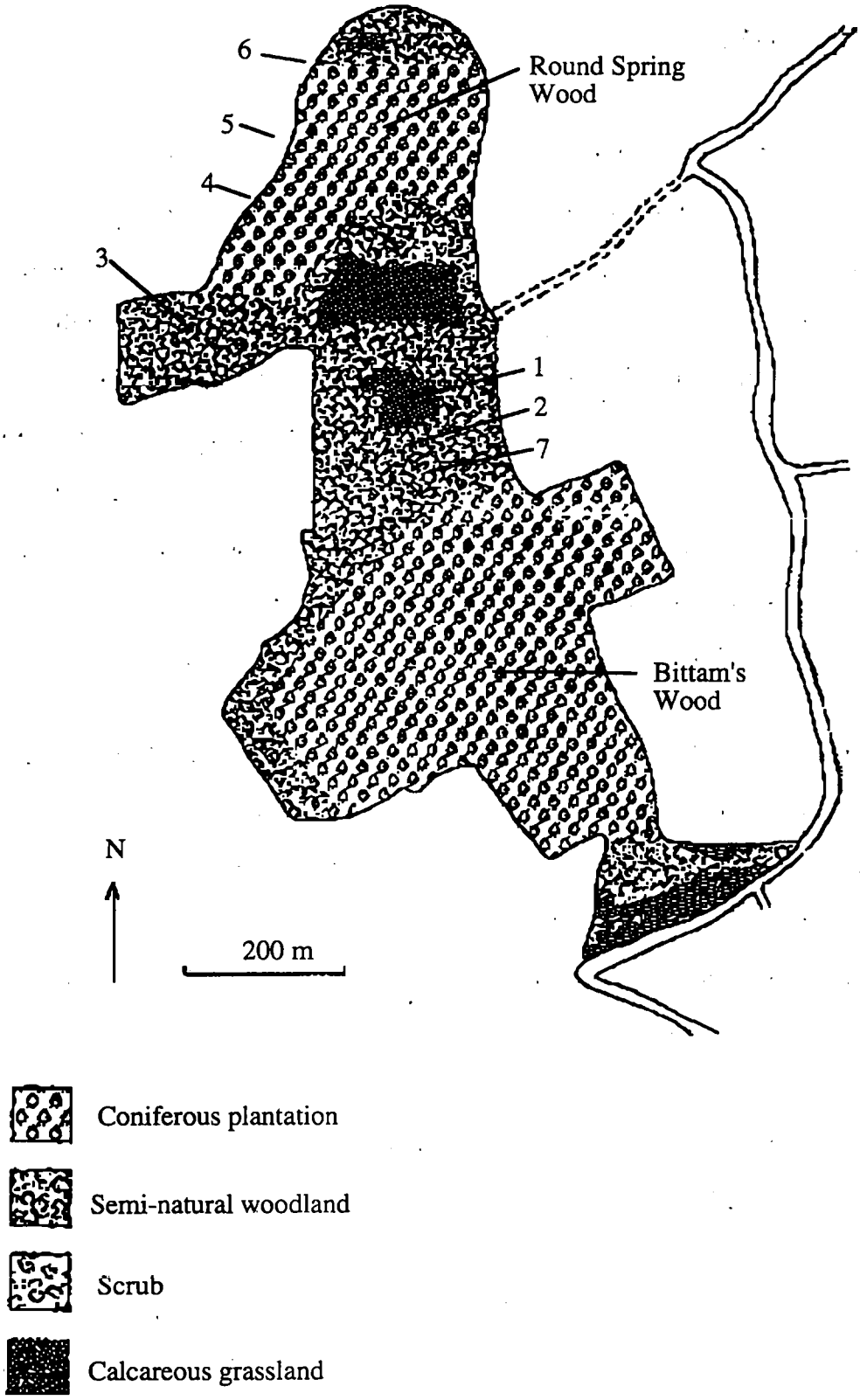
Broad leaved species with a coniferous nurse crop were planted afterwards, and those areas are currently being managed by the Forestry Commission. The few patches that are kept as grasslands are floristically rich, with several orchid species and seven unimproved calcareous grassland indicator species being present.

The rest of the reserve, where most of the studied *P. vulgaris* populations lay, is covered by a semi-natural beech/ash wood (*Fagus sylvatica / Fraxinus exelsior*). Other tree species such as birch (*Betula pendula* and *B. pubescens*), sycamore (*Acer pseudoplatanus*), field maple (*Acer campestre*), cherry (*Prunus avium*), whitebeam (*Sorbus aria*) and goat willow (*Salix caprea*) are found throughout the reserve. Some stands also have pedunculate oak (*Quercus robur*) and holly (*Ilex aquifolium*). The ground flora is characteristic for its richness and diversity, including 29 ancient woodland indicator species among which *Primula vulgaris*, *Conopodium majus* (pignut), and *Daphne laureola* (spurge laurel) are frequent. The dominant species of this ground layer are *Mercurialis perennis* (dog's mercury), *Hyacinthoides non-scripta* (bluebell) and *Galium odoratum* (woodruff).

This area has traditionally been managed through coppice cycles of 5 to 10 years, the coppiced species being mainly hazel (*Corylus avellana*) and hawthorn (*Crataegus monogyna*). The type of woodland present in the study sites conforms to W8, *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland, with some stands closer to W12, *Fagus sylvatica-Mercurialis perennis* woodland, according to the National Vegetation Classification (Rodwell 1991).

The soils of the reserve fall into three major groups: 1) brown earth, which is basically derived from clay-with-flints, is found in most of Bittam's Wood (Fig. 2.3); it is a considerably acid deep clay with flints, with pH values of around 4.3 at 3cm deep; 2) brown calcareous soils are yellow-red clay with chalk fragments, 1.30 to 1.50m deep, mainly occurring in Round Spring wood; and 3) rendzinas, which are common in the grassland near Round Spring Wood and the surrounding forested areas; however, in most

Figure 2.3 General vegetation map of Dancers End Reserve (from MSC Management Plan Team, 1988). The numbers indicate the approximate location of the seven populations studied.



beechwood rendziniforme soil is modified and has a dark humose horizon at the surface that grades into a lighter yellow-brown silt loam. Most of the semi-natural woodland is on transitional soils (between 2 and 3) that are slightly alkaline (pH of around 8 at 3 cm). The soil of the reserve does not rest on solid chalk directly. The parent material is either clay-with-flints or chalk brash, consisting of angular chalk fragments in a chalky matrix (Radford 1986, cited in MSC Management Plan Team, 1988).

I chose seven *P. vulgaris* populations along a range of light conditions in Dancers End Reserve to carry out the field work of this research project. The approximate location of each studied patch is marked in Fig. 2.3. Three patches (4, 5 and 6) are located in beech/ash forest outside the reserve boundaries, in the buffer semi-natural woodland that surrounds the area.

2.2.2 Woburn Wood

Additional field work was conducted at Lowe's Wood, a hardwood forest within the land managed by Bedford Estates in Woburn Wood, Bedfordshire, to the south of Milton Keynes (Grid Reference SP 927 325). The vegetation type in this area corresponds to W10, *Quercus robur-Pteridium aquilinum-Rubus fruticosus* woodland, according to the National Vegetation Classification (Rodwell 1991). The dominant tree species are *Quercus robur* (pedunculate oak) and *Castanea sativa* (chestnut), and the shrub layer is composed mainly of hazel (*Corylus avellana*) and hawthorn (*Crataegus monogyna*). At the ground level dense stands of *Pteridium aquilinum* (bracken) are ubiquitous during summer. The presence of *P. vulgaris* at this site seem to be correlated with the dampness of the soil and with soil type, which in this part of the forest is clay, as opposed to the sandy composition that predominates in the surrounding area.

2.2.3 Salcey Forest

Another population was studied in Salcey Forest, an oak/ash wood to the south of Northampton (Grid Reference SP 814 508). This area belongs to the Forestry Commission and is mainly planted with coniferous woodland. However, a small part of it is a reserve of hardwood forest, managed by The Northamptonshire Wildlife Trust.

The reserve comprises 14 hectares (34 acres) on boulder clay, and is dominated by a tree layer of *Quercus robur* (pedunculate oak) that was planted in the middle of the last century. Other important tree species are *Fraxinus exelsior* (ash), *Acer campestre* (field maple), *Acer pseudoplatanus* (sycamore) and the introduced *Quercus cerris* (Turkey oak) and *Castanea sativa* (sweet chestnut). The shrub layer is composed by coppice growth of *Corylus avellana* (hazel), *Acer campestre* (field maple), and *Crataegus monogyna* (hawthorn) and important elements of the ground flora are *Dryopteris filix-mas* (the male fern), *Primula vulgaris*, *Hyacinthoides non-scripta* (bluebell) and *Hedera helix* (ivy) (Colston *et al.* 1987).

Chapter 3. Variation in the Demography of *Primula vulgaris* along the Forest Regeneration Cycle

3.1 Introduction

Woodlands are dynamic systems. The opening and closure of canopy gaps are a recurring source of environmental heterogeneity, resulting in a mosaic of regenerating patches of different sizes and ages occurring simultaneously at a site (Brokaw 1985b; Pickett and White 1985; Runkle and Yetter 1987). This habitat heterogeneity allows the co-existence of species with different life histories and ecological requirements, which contributes to the maintenance of species diversity (Barkham 1992a). In particular, the opening of gaps in the canopy allows the establishment of many understory species. However, gaps close as canopy regeneration proceeds. To understand how forest herbs persist in such dynamic conditions, we need to consider ecological processes at two different spatial scales: 1) at the level of the demography of local populations occupying individual forest patches, and 2) at the level of the forest as a whole, understood as a metapopulation formed by a set of local populations. This chapter addresses the first of these levels and concentrates on the demography of local populations of *Primula vulgaris*. However, it should be viewed within the larger-scale metapopulation scope that is the main theme of my thesis, as the understanding of the dynamics of local populations will ultimately shed light on relevant ecological processes occurring at the metapopulation level.

Like *P. vulgaris*, many woodland herbs colonise the clearings produced by the opening of gaps in the canopy. The demography of such species has been much studied (Bierzychudek 1982a, 1982b; Collins *et al.* 1985; Kawano *et al.* 1987; Barkham 1992b). However, the ephemeral character of their habitat patches, determined by the closure of canopy gaps as

adjacent vegetation grows into them, has been largely overlooked. Relatively little is known about the effect of the environmental changes brought about by this successional process on the demography of herb populations.

Horvitz and Schemske (1986) studied the demography of a tropical forest herb, *Calathea ovandensis*, under relatively open conditions and modeled the demographic changes that would occur due to canopy closure based on observations of the behaviour of populations under closed canopy conditions. Cipollini *et al.* (1993) published a similar analysis for *Cynoglossum virginianum*, a temperate forest herb. In both studies, projection matrices were built for hypothetical populations along the forest regeneration cycle, though actual data was collected for only one and three populations, respectively. Other studies on the subject have obtained actual field estimates of the demographic response of forest species to secondary succession, but have mainly concentrated on tropical trees (i.e., *Cecropia obtusifolia* and *Astrocaryum mexicanum* - Martínez-Ramos *et al.* 1985; Alvarez-Buylla and García-Barrios 1991; Alvarez-Buylla 1994).

Horvitz and Schemske (1986) and Cipollini *et al.* (1993) illustrated the effect that canopy closure might have on the demography of gap-dependent herbs. However, both studies used interpolated rather than empirical parameter values to account for the effect of canopy closure on population dynamics, as no complete data set for the demography of these forest herbs in forest patches of different type was available. The primary aim of this chapter is to illustrate how the demography of *P. vulgaris* populations is affected by the dynamics of the forest canopy. To such end, nine populations were studied across a range of light conditions, corresponding to different stages of the canopy regeneration cycle. The knowledge of the dynamics of individual local populations in patches with different light environments offers insights into the ecological processes that affect population extinction and colonisation, and will therefore aid in the understanding of the functioning of the metapopulation as a whole.

3.2 Materials and Methods

Nine *P. vulgaris* populations along a range of light conditions were chosen for study: seven at Dancers End reserve, including one in a grassland area (referred to as DE1, DE2, etc.), one at Salcey Forest (SF), and one at Woburn Wood (WW). A description of the three sites was given in Chapter 2.

3.2.1 Light Measurement

The diffuse light (diffuse site factor, measured as the percentage of open sky - Anderson 1964; Mitchell and Whitmore 1993) was used to characterise the light environment at each patch. The details about the methodology followed to take and analyse the photographs are explained in Chapter 4 (section 4.2.1). Photographs were taken in each patch during the same time and in exactly the same points in summer 1992, 1993, and 1994. The mean diffuse light of 7 to 15 photographs per year was used to describe the light environment of each population.

3.2.2 Population Sampling

Demographic data was obtained from samples of approximately 300 plants per population, followed from 1992 through 1994. In May, 1992 I set permanent one square-metre quadrats regularly spaced along a transect passing through the centre of each patch. The number of quadrats per population ranged between 8 and 32, depending on the density of *P. vulgaris* plants in each case. The four corners of each quadrat were marked by plastic pipes sunk into the ground.

The quadrats represent a grid in which plants were located through x and y coordinates along the horizontal and vertical axis, respectively. This allowed me to relocate plants each

year and record their relevant attributes (see below) as well as note missing plants, which were considered dead.

Populations were sampled between the end of May and the beginning of July in 1992, 1993 and 1994, at the time when plants had developed to their full size and their capsules were ripening. Each year all plants in the quadrats were recorded, their leaves, rosettes and capsules counted and their area estimated as an ellipse, based on their longer diameter, a, and a perpendicular diameter, b (area= $\pi\ a/2\ \ b/2$).

All new seedlings in the quadrats were counted and their positions recorded. They were marked with a small straw ring for re-location the following year. In quadrats with a high number of seedlings, only some of them were marked to be followed the year after.

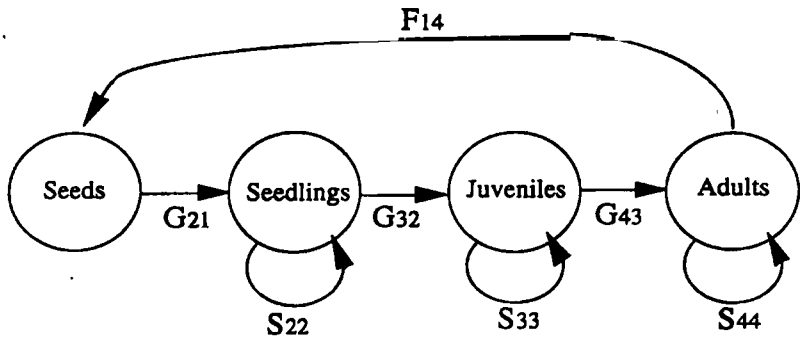
These records gave detailed information about the fate of each individual plant in the sample from one year to the next. By comparing the state of each plant at two given times I was able to build population projection matrices for two growth periods: 1992-93 and 1993-94.

3.2.3 Projection Matrices

- Matrix Analysis

A population projection matrix is, in essence, an expression of a life table. The construction of a matrix involves the recognition of differences between individuals in a population, taking into account that their fate can potentially be related to age, size, stage, sex or other variables (Caswell 1978). Lefkovitch matrices, in particular, are based on the sub-division of populations in stage categories and have been adapted to analyse the demography of populations with complex life cycles (Caswell 1989). A population projection matrix is a convenient way of expressing systems of equations that describe the transitions of individuals among the different stage categories during a given period of time.

Figure 3.1 Correspondence between the life cycle graph and a Lefkovitch matrix. The circles in the diagram represent stage categories and the arrows show contributions or transitions among them (Fecundity, Survival and Growth entries).



$$A = \begin{array}{c} \\ \text{Stage at time t+1} \end{array} \begin{array}{c} \begin{array}{cccc} \text{Se.} & \text{Sdls.} & \text{Juv.} & \text{Ads.} \end{array} \\ \begin{bmatrix} 0 & 0 & 0 & F_{14} \\ G_{21} & S_{22} & 0 & 0 \\ 0 & G_{32} & S_{33} & 0 \\ 0 & 0 & G_{43} & S_{44} \end{bmatrix} \end{array}$$

Stage at time t

In order to build a matrix for a given population, it is important to understand the correspondence between the organism's life cycle graph and its transition and fecundity matrix. Let us picture, for instance, a population sub-divided into four stage classes like the one in Fig. 3.1. Each circle represents a stage category and each arrow shows the possible connecting routes between stage categories, which represent the contributions or transitions of individuals from one stage category to another occurring in one time step. The number of stage categories in which the population is sub-divided determines the dimensions of the square matrix and the arrows represent the actual matrix entries, as illustrated in Fig. 3.1.

The structure of a population can be described in terms of the number of individuals in each stage class at a given time by a vector $\mathbf{n}_t$. A matrix, **A**, describes the transition probabilities of individuals between stage classes: each matrix entry, a_{ij}, represent the transitions or contributions of individuals from the *j*-th class to individuals in the *i*-th class in one time step. Multiplying **A** by $\mathbf{n}_t$ will result in a new vector, $\mathbf{n}_{t+1}$, that describes the structure of the population after one year:

$$\underset{\mathbf{A}}{\begin{pmatrix} 0 & 0 & 0 & F_{14} \\ G_{21} & S_{22} & 0 & 0 \\ 0 & G_{32} & S_{33} & 0 \\ 0 & 0 & G_{43} & S_{44} \end{pmatrix}} \times \underset{\mathbf{n}_t}{\begin{pmatrix} P_1 \\ P_2 \\ P_3 \\ P_4 \end{pmatrix}} = \underset{\mathbf{n}_{t+1}}{\begin{pmatrix} P'_1 \\ P'_2 \\ P'_3 \\ P'_4 \end{pmatrix}} \qquad (1)$$

If matrix **A** is multiplied again by vector $\mathbf{n}_{t+1}$, a new vector is obtained. If this process is iterated several times the proportions of the resulting vector will eventually remain constant. The population structure given by such a vector corresponds to the stable stage distribution, i.e., the number of individuals in each category at equilibrium. In matrix terms, this corresponds to the dominant right eigen-vector of the matrix, **w**, which has the property that

$$\mathbf{A} \times \mathbf{w} = \lambda \times \mathbf{w} \qquad (2)$$

for a particular eigen-value, $\lambda > 0$. In other words, multiplying matrix **A** by the vector **w** is equivalent to multiplying the vector by a scalar, λ. This eigen-value, called the dominant eigen-value of the matrix, is a positive constant that describes population growth rate, defined in demographic terms in relation to r, the malthusian parameter or intrinsic rate of natural increase

$$r = \ln \lambda \qquad (3)$$

Population growth rate, λ, has been widely used in demographic and evolutionary studies since it was first described by Fisher in 1930 as the mean fitness of a population (Caswell 1978). $\lambda = 1$ represents a population at equilibrium; $\lambda < 1$ indicates a decreasing population and $\lambda > 1$ represents a growing population.

Another important parameter is the left eigen-vector, **v**, satisfying the following conditions:

$$\mathbf{v}' \times \mathbf{A} = \lambda \times \mathbf{v}' \qquad (4)$$

where $\mathbf{v}'$ is the transpose of **v**. This left eigen-vector corresponds to the reproductive value, i.e., the present value of the future offspring of individuals in each stage category (Caswell

1989). Note that λ, **w**, and **v** are properties of matrix **A** and do not depend on the initial conditions, $\mathbf{n}_t$.

- Parameter Estimation

a) Stage Categories

Population projection matrices were built for the nine populations studied. *P. vulgaris* survival, growth, and fecundity are clearly affected by the stage or size of plants (Boyd 1986), as is the case for most plant species (Werner and Caswell 1977). Therefore, stage categories based on size and on other stage-related attributes were defined to model population dynamics.

Two sources of error must be considered when subdividing a population into stage categories. Subdivision of the population into many categories could lead to errors related to small sample sizes within each class. However, subdividing the population into few, large categories would provide little demographic detail and could overlook potentially biased distributions of individuals within categories (Vandermeer 1978; Moloney 1986). The best choice would be to determine a number of categories that minimise both sources of error. Vandermeer (1978) and Moloney (1986) have proposed an algorithm that calculates the optimum number of categories as well as their limits under these considerations.

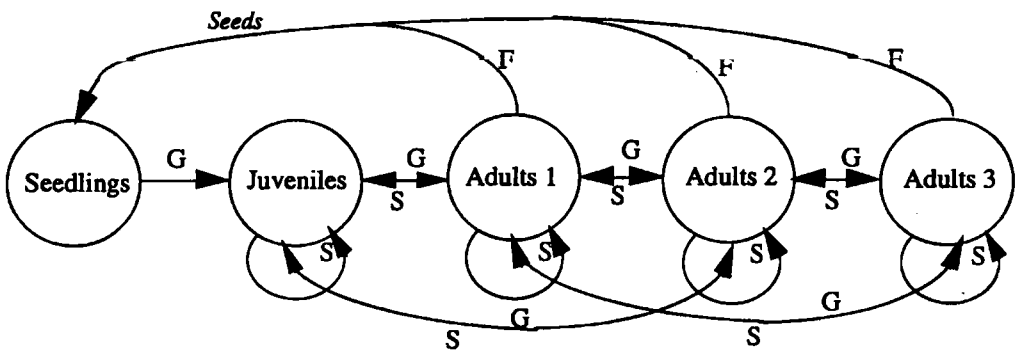
In this work the choice of stage categories was done through the knowledge of the behaviour of plants in natural conditions after three years of observation, e.g., the approximate size at which seedling become established or plants start reproducing. Five categories, reflecting natural stages and apparent threshold size values for reproduction (Menges 1990), were determined as shown in Table 3.1. This number of categories provided enough 'demographic resolution' for the purposes of this work, and the sample sizes within categories were large enough (each containing a minimum of 10 individuals) to allow satisfactory estimates of transition probabilities between categories.

Table 3.1 Stage categories chosen to describe the population dynamics of *P. vulgaris*.

Category	Plant Size (Area in cm^2)	Stage
Seedlings	0.5 to 5	cotyledons present
Juveniles	5.1 to 35	non reproductive
Adults 1	35.1 to 200	potentially reproductive
Adults 2	200.1 to 600	potentially reproductive
Adults 3	larger than 600	potentially reproductive

The life cycle graph of *P. vulgaris* shows the main possible transitions between stage categories and their correspondence with the population projection matrix (Fig. 3.2).

Figure 3.2 Life cycle graph of *P. vulgaris* and its correspondence with 'fecundity' (F), 'growth' (G) and 'survival' (S) matrix entries.



Stage at time t

Stage at time t+1	Sd.	J	A1	A2	A3
Sd.	0	0	F	F	F
J	G	S	S	S	0
A1	0	G	S	S	S
A2	0	G	G	S	S
A3	0	0	G	G	S

Seedlings can either die or become juveniles in one year's time (in very few occasions did seedlings grew as fast as to reach the adult 1 category in one year). The juveniles and the three adult categories can experience several possible fates, such as remaining in the same category, growing one or two categories, or shrinking one or two categories. Adults contribute to the next generation of seedlings through the production of seeds, all of which either germinate to produce new seedlings, or die (as *P. vulgaris* seeds do not remain viable in the soil for long periods of time - Boyd *et al.* 1990; Valverde and Silvertown, in press, Appendix A). The following sections describe how matrix entries, corresponding to the arrows in Fig. 3.2, were calculated.

b) Transition Probabilities and Mortality

A frequency table was built to obtain the probability of individuals changing categories in one year's time. This was done by counting the number of individuals in each category experiencing each particular fate from one year to the next, including death (Table 3.2).

Table 3.2 An example of a frequency table.

	Category at time t				
Fate at t+1	Seedlings	Juveniles	Adult 1	Adult 2	Adult 3
Seedlings	0	0	0	0	0
Juveniles	35	54	4	2	0
Adult 1	0	40	38	7	0
Adult 2	0	8	35	48	14
Adult 3	0	0	1	12	11
Death	8	4	1	1	0
Total (N_t)	43	106	79	70	25

Mortality and transition probabilities can be obtained directly from the frequency table by calculating the proportion of individuals in each category following the different possible fates. The result is the transition matrix shown in Table 3.3. Note that death is a fate in the frequency table, but is not explicitly included as part of the transition matrix.

Table 3.3 Transition matrix and mortality per category (from frequency data in Table 3.2)

	Category at time t				
Fate at t+1	Seedlings	Juveniles	Adult 1	Adult 2	Adult 3
Seedlings	0	0	0	0	0
Juveniles	0.814	0.509	0.050	0.029	0
Adult 1	0	0.377	0.481	0.100	0
Adult 2	0	0.076	0.443	0.686	0.560
Adult 3	0	0	0.013	0.171	0.440
Q_x	0.186	0.038	0.013	0.014	0
	1	1	1	1	1

c) Fecundity

Fecundity is the mean number of offspring per reproductive plant at a given time that joins the population the following growth season. Two approaches can be used to estimate this parameter. The 'empirical' approach allocates the number of seedlings recruited to the various categories according to their proportional reproductive effort and to the number of individuals which belonged to each category during the previous reproductive season. The 'mechanistic' approach, on the other hand, attempts to analyse all the components of fecundity using detailed data on flower production, seed set, field seed germination and seedling emergence (Alvarez-Buylla 1986; Menges 1990). In this study both approaches were used. Empirical fecundities were calculated for both 1992-93 and 1993-94 data sets, and mechanistic fecundities only for the 1993-94 period.

Empirical fecundity:

I estimated the proportional contribution of each adult category to total reproductive effort, measured as total number of capsules. The total number of seedlings counted the following year in the sample quadrats were allocated to the different adult categories according to their proportional reproductive effort. Finally, the number of recruitments per category was divided by the total number of individuals in each category to obtain the mean fecundity per category. An example is given in Table 3.4.

Table 3.4 Calculation of the fecundity using the empirical approach (for matrix in Table 3.3)

	Total	Adults 1	Adults 2	Adults 3
Contribution, per category, to total no. of capsules	256	43	151	62
Proportion per category	1	0.168	0.590	0.242
Seedlings recruited in t+1	595	99.96	350.93	144.11
No. of individuals per category at time t	174	79	70	25
Mean Fecundity per category		**1.265**	**5.013**	**5.764**

Mechanistic fecundity:

The mechanistic approach took a closer examination of the various processes that determined fecundity, particularly seed set and seedling emergence in natural conditions. In order to estimate the average number of seeds produced per flower and per capsule, the flowers of 20 reproductive plants chosen at random were marked in each population in May 1993. The resulting capsules were collected and their seeds counted.

The emergence of seedlings from a known number of seeds was also estimated. Ten 10x10cm quadrats were marked on the ground along a transect in each population. In each of five quadrats, fifty seeds were scattered on the ground in July 1993. No seeds were sown in the other five quadrats. The number of seedlings per quadrat was recorded in May, 1994. The number of seedlings in the control quadrats was subtracted from the number of seedlings in the seeded quadrats before calculating the percentage of seedling emergence.

The mechanistic estimation of fecundities for this period involved recording the number of capsules per category and estimating seed set according to the data on mean number of seeds per capsule for each population. The number of seeds produced per individual in each category was obtained by dividing the estimated total number of seeds per category by the number of individuals in each category. Finally, the percentage of those seeds becoming

seedlings the following year was estimated using the percentage of seedling emergence obtained for each population in the 10x10cm quadrat experiment described above. An example is given in Table 3.5

Table 3.5 Sample calculation of mechanistic fecundities for a population in which the number of seeds per capsule was 30.35 and the percentage of seedling emergence was 4.8%.

	Total	Adults 1	Adults 2	Adults 3
No. of Capsules in 1993	730	56	456	218
Estimated No. of seeds *(seeds/capsule = 30.35)*	22,155.5	1,699.6	13,839.6	6,616.3
No. of individuals	214	85	105	24
Seeds per individual		19.99	131.81	275.68
Seedlings emerging in 1994 per individual *(% seedling emergence = 4.8%)*		**0.959**	**6.327**	**13.233**

d) Determination of Demographic Parameters

The demographic parameters λ (population growth rate), **w** (stable stage distribution) and **v** (reproductive value) for the projection matrices were calculated as the dominant eigen-value, the dominant right eigen-vector and the dominant left eigen-vector, respectively. A computer program written by E.R. Alvarez-Buylla was used to perform these analysis. This program also calculates the sensitivity and elasticity matrices, as described below.

e) Sensitivity and Elasticity Analysis

The sensitivity and elasticity concepts were explained in Chapter 1. The sensitivity matrix is built by calculating the sensitivity of each entry of the population projection matrix, a_{ij}, as

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \qquad (5)$$

which measures the impact on λ of a small change in the transition a_{ij} relative to similar changes in other elements of the matrix (Caswell 1978; de Kroon *et al.* 1986). Elasticity, a measure of proportional sensitivity, is given by

$$e_{ij} = \frac{a_{ij}}{\lambda} \times \frac{\partial \lambda}{\partial a_{ij}} \qquad (6)$$

which gives the proportional contribution of each element of the matrix, a_{ij}, to λ (de Kroon *et al.* 1986).

- Statistical Treatment of Matrix Results

a) Comparison of Population Structures

Differences between population structures (observed *vs.* calculated stable distributions, observed structures between different years, and calculated stable distributions between different years) were evaluated using the log likelihood ratio, G (Sokal and Rohlf 1981; Zar 1984). This G ratio, a more robust alternative than χ^2 to evaluate goodness of fit, was estimated as

$$G = 2 \left(\sum_{i=1,i=n} f_i \ln f_i - \sum_{i=1,i=n} f_i \ln f^*_i \right) \qquad (7)$$

where f_i are the observed frequencies and f^*_i are the calculated frequencies (Zar 1984).

b) Log-linear Analysis of Population Structure and Matrices

One of the approaches used to evaluate the statistical significance of demographic differences between populations in different patches and/or at different times involves comparing entire transition matrices. This can be done using log-linear analysis of contingency tables to evaluate the degree of interdependence between the explanatory and the response factors involved. I used this method to determine the significance of the effect of time (years) and forest patch (population) on population structure and transition matrices (Caswell 1989; Silva *et al.* 1990; Ehrlen 1995; Horvitz and Schemske 1995).

To compare the observed structure among all populations for the three periods studied (1992, 1993 and 1994), a log-linear analysis of a three-way contingency table was performed. The explanatory factors used were patch and year, whereas the observed frequency of individuals per category was the response factor. To compare entire transition matrices, a log-linear analysis of a four-way contingency table was done using year, patch,

and initial category as explanatory variables, and the fate of individuals as the response variable. A detailed explanation of the methodology I followed is given in Appendix B.1, along with the main results of the analysis.

c) Confidence Intervals for Population Growth Rate

Estimation of individual matrix entries from field data necessarily implies associated errors. As λ is calculated in terms of those vital rates, there must also be uncertainty associated with the estimate of λ. However, there appears to be no general formula describing the distribution of λ in terms of the a_{ij}, nor an expression for the variance of λ as a function of the variance of the a_{ij} (Caswell 1989; Alvarez-Buylla and Slatkin 1991). Two approaches have been developed to address this matter. An analytical method uses the sensitivity formula to estimate an approximate variance of λ. Confidence intervals are then calculated from this variance assuming a normal distribution. A second approach uses computer re-sampling methods to estimate non-parametric confidence intervals by repeatedly calculating λ from sub-samples of the original data set (bootstrap and jack-knife - Caswell 1989).

The analytical method was used in this study to estimate the approximate confidence intervals for λ, as it is more readily available. This method is reliable provided that the coefficients of variations for matrix entries to which λ is very sensitive are sufficiently low (less that 50% - Alvarez-Buylla and Slatkin 1993, 1994). According to this method, the approximate variance of λ is given by

$$V(\lambda) = \sum_{i,j} \left(\frac{\partial \lambda}{\partial a_{ij}}\right)^2 V(a_{ij}) + \sum_{i,j \neq k,j} \left(\frac{\partial \lambda}{\partial a_{ij}}\right) \left(\frac{\partial \lambda}{\partial a_{kj}}\right) COV\,(a_{ij}, a_{kj}) \qquad (8)$$

as defined by Alvarez-Buylla and Slatkin (1994). The first term of eq. (8) is equivalent to the equation proposed by Lande (1988) and Caswell (1989) to estimate the variance of λ, which did not consider the effect of covariances. Thus, the second term in eq. (8) accounts for the covariance between pairs of transitions from the same initial category to any other category (a_{ij} and a_{kj}). Negative correlations are expected between these pairs of transitions

because if, for instance, the probability of remaining in the same category is overestimated, the probability of passing to any other category will be underestimated (Alvarez-Buylla and Slatkin 1991, 1993, 1994).

The variance of fecundity entries was calculated using the information on the natural variability in this parameter obtained directly from the empirical demographic data collected in different populations (Lande 1988; Alvarez-Buylla and Slatkin 1991). As transition probabilities show a binomial distribution, their variance was calculated as

$$V(a_{ij}) = a_{ij} \frac{(1-a_{ij})}{n} \qquad (9)$$

Sampling covariances between pairs of transitions from the same initial category were estimated according to the multinomial distribution (Alvarez-Buylla and Slatkin 1991) as follows:

$$COV\ (a_{ij}, a_{kj}) = \frac{(-(a_{ij})\ (a_{kj}))}{n} \qquad (10)$$

Standard error (σ) was calculated as the square root of the variance of λ, as obtained from eq. (8). Approximate 95% confidence intervals were calculated as $\lambda \pm 2\sigma$.

3.3 Results

3.3.1 Light Measurement

A summary of the light measurements given by the analysis of the hemispherical photographs is presented in Table 3.6. Note that one of the populations in Dancers End (DE1), had over 90% diffuse light, much higher than the rest. This population was in a grassland. Despite being an atypical environment for *P. vulgaris*, some populations do establish in such habitats. I studied this population to compare the demographic behaviour of *P. vulgaris* in such conditions with those in the forest.

The woodland patches studied cover the full range of light conditions in which *P. vulgaris* populations usually occur, from a big gap in the canopy (13.21% openness), to completely closed canopy conditions (1.57% openness). The light in each patch changed from year to year. In general, light decrease was more noticeable in brighter patches, whereas the light conditions in darker patches remained approximately constant. These data are further analysed in Chapter 4.

Table 3.6 Results of the light measurements for *P. vulgaris* populations at Dancers End (DE), Woburn Wood (WW) and Salcey Forest (SF). Populations are listed in order of decreasing diffuse light. The mean diffuse light (and standard deviation) were calculated from a varying number (n) of hemispherical photographs per population.

Population	Diffuse light (% canopy openness)			
	1992	1993	1994	n
DE1	94.76 (1.23)	93.47 (1.47)	93.66 (1.24)	7
DE7	—	13.21 (4.44)	11.16 (3.14)	7
DE2	12.01 (2.20)	9.12 (1.73)	7.31 (2.82)	8
DE5	5.95 (2.09)	4.88 (1.53)	3.16 (1.75)	7
WW	5.65 (2.92)	4.78 (3.13)	4.05 (2.48)	15
SF	3.09 (1.28)	3.08 (1.73)	1.90 (1.00)	11
DE3	2.67 (1.36)	1.87 (0.88)	1.84 (0.60)	8
DE4	2.03 (0.71)	1.95 (0.58)	1.46 (0.72)	7
DE6	1.57 (0.79)	1.97 (0.81)	—	7

3.3.2 Projection Matrices

Projection matrices for the eight populations studied during the periods 1992-93 and 1993-94 are presented in Table 3.7, along with the main results of matrix analysis (λ, stable stage distribution, and reproductive values). Matrices are presented in order of decreasing diffuse light. Population DE6 was only studied from 1992 to 1993 because the forest was cut down in that area at the end of 1993. Population DE7 was added during the second period.

Note that the projection matrices for the grassland population (DE1) have only four stage categories. These matrices were built using the same stage categories as for the other populations but no adults over 600cm^2 were found (Table 3.1). Individuals growing in open conditions tend to be smaller than those growing under the canopy. These differences in environmental and biotic conditions make demographic comparisons between grassland and woodland habitats difficult (and perhaps pointless). Thus population DE1 was excluded from some of the analyses presented below.

Table 3.8 compares the results of the empirical and mechanistic approaches to calculate matrix fecundity for the period 1993-94. Mechanistic fecundities were consistently larger than the empirical ones, therefore producing higher λ values. The difference between the results of the two approaches was more noticeable in populations with higher λ. However, regardless of the method used to estimate fecundity, λ values were higher in the first period (1992-93) than for the second one (1993-94) (Table 3.7).

Table 3.7 Population projection matrices and main demographic results of the matrix analysis for the nine populations studied during the periods **1992-93** (a) and **1993-94** (b). n_{t+1} refers to the observed structure of populations in 1993 (a) and in 1994 (b). n refers to the number of individuals considered to calculate the transitions in each matrix column. Diagonal matrix elements are underlined and fecundity entries are bold to facilitate reading. Diffuse light values were obtained in summer, 1992 (a) and 1993 (b).

Table 3.7a	**1992-93** Seedl.	Juv.	Adult 1	Adult 2	Adult 3	n_{t+1}	Stable stage distribution	Reprod. Value
DE1	**λ=1.622**		Diff. light= 94.76					
Seedl.	0.000	0.000	**3.027**	**5.764**		0.658	0.444	0.066
Juv.	0.814	0.509	0.040	0.000		0.105	0.332	0.132
Adult 1	0.000	0.453	0.859	0.560		0.210	0.208	0.324
Adult 2	0.000	0.000	0.087	0.440		0.027	0.015	0.477
n	43	106	149	25				
DE2	**λ=1.976**		Diff. light= 12.01					
Seedl.	0.000	0.000	**4.469**	**22.904**	**44.898**	0.900	0.634	0.014
Juv.	0.588	0.423	0.025	0.000	0.000	0.033	0.241	0.042
Adult 1	0.021	0.454	0.562	0.120	0.000	0.032	0.089	0.128
Adult 2	0.000	0.0210	0.375	0.780	0.630	0.029	0.033	0.318
Adult 3	0.000	0.000	0.000	0.100	0.333	0.005	0.002	0.498
n	97	97	80	50	27			
DE5	**λ=1.794**		Diff. light= 5.95					
Seedl.	0.000	0.000	**2.136**	**5.463**	**13.140**	0.811	0.598	0.031
Juv.	0.444	0.328	0.030	0.000	0.000	0.028	0.183	0.080
Adult 1	0.111	0.492	0.310	0.025	0.000	0.042	0.107	0.177
Adult 2	0.000	0.115	0.570	0.658	0.317	0.077	0.081	0.270
Adult 3	0.000	0.000	0.090	0.304	0.682	0.042	0.031	0.441
n	18	61	100	79	63			
WW	**λ=0.974**		Diff. light= 5.65					
Seedl.	0.000	0.000	**0.026**	**0.092**	**0.303**	0.080	0.055	0.104
Juv.	0.429	0.273	0.040	0.007	0.000	0.056	0.066	0.171
Adult 1	0.143	0.545	0.661	0.326	0.000	0.415	0.503	0.199
Adult 2	0.000	0.045	0.210	0.619	0.540	0.390	0.348	0.241
Adult 3	0.000	0.000	0.008	0.034	0.405	0.059	0.028	0.285
n	10	22	124	147	37			

SF	**λ=1.035**		Diff. light= 3.09					
Seedl.	0.000	0.000	**0.015**	**0.063**	**0.189**	0.072	0.107	0.090
Juv.	0.294	0.250	0.000	0.000	0.000	0.050	0.041	0.188
Adult 1	0.176	0.350	0.385	0.059	0.012	0.143	0.086	0.216
Adult 2	0.000	0.300	0.461	0.568	0.171	0.377	0.287	0.241
Adult 3	0.000	0.000	0.108	0.356	0.805	0.358	0.482	0.264
n	17	20	65	118	82			
DE3	**λ=1.055**		Diff. light= 2.67					
Seedl.	0.000	0.000	**0.037**	**0.144**	**0.231**	0.096	0.128	0.071
Juv.	0.385	0.305	0.041	0.000	0.000	0.071	0.072	0.195
Adult 1	0.000	0.639	0.377	0.037	0.046	0.200	0.111	0.227
Adult 2	0.000	0.055	0.531	0.626	0.231	0.387	0.333	0.248
Adult 3	0.000	0.000	0.041	0.336	0.723	0.246	0.356	0.258
n	13	36	98	107	65			
DE4	**λ=1.267**		Diff. light= 2.03					
Seedl.	0.000	0.000	**0.332**	**0.514**	**1.020**	0.316	0.318	0.092
Juv.	0.200	0.167	0.039	0.000	0.000	0.038	0.065	0.166
Adult 1	0.400	0.474	0.364	0.079	0.000	0.152	0.191	0.210
Adult 2	0.000	0.278	0.351	0.476	0.264	0.229	0.187	0.243
Adult 3	0.000	0.055	0.234	0.444	0.717	0.265	0.239	0.288
n	10	18	77	63	53			
DE6	**λ=1.133**		Diff. light= 1.57					
Seedl.	0.000	0.000	**0.121**	**0.297**	**0.620**	0.194	0.202	0.097
Juv.	0.375	0.400	0.009	0.012	0.000	0.071	0.110	0.156
Adult 1	0.250	0.556	0.459	0.165	0.019	0.260	0.233	0.205
Adult 2	0.000	0.000	0.396	0.588	0.211	0.287	0.249	0.241
Adult 3	0.000	0.000	0.099	0.223	0.750	0.188	0.205	0.300
n	16	45	111	85	52			

Table 3.7 b	**1993-94** Seedl.	Juv.	Adult 1	Adult 2	Adult 3	n_{t+1}	Stable stage distribution	Reprod. Value
DE1	**λ= 1.294**		Diff. light= 93.49					
Seedl.	0.000	0.000	**1.041**	**3.509**		0.461	0.411	0.051
Juv.	0.516	0.621	0.037	0.000		0.162	0.324	0.127
Adult 1	0.000	0.253	0.674	0.167		0.255	0.160	0.319
Adult 2	0.000	0.011	0.279	0.833		0.122	0.104	0.503
n	64	95	190	24				
DE7	**λ= 0.868**		Diff. light= 13.21					
Seedl.	0.000	0.000	**0.035**	**0.230**	**1.073**	0.201	0.133	0.050
Juv.	0.441	0.340	0.092	0.060	0.000	0.187	0.204	0.078
Adult 1	0.051	0.245	0.494	0.298	0.139	0.293	0.369	0.169
Adult 2	0.000	0.000	0.195	0.500	0.500	0.253	0.252	0.277
Adult 3	0.000	0.000	0.000	0.083	0.361	0.066	0.041	0.425
n	59	53	87	84	36			
DE2	**λ= 1.229**		Diff. light= 9.12					
Seedl.	0.000	0.000	**0.543**	**6.480**	**18.610**	0.747	0.625	0.009
Juv.	0.200	0.490	0.082	0.011	0.000	0.070	0.182	0.052
Adult 1	0.008	0.270	0.660	0.112	0.000	0.086	0.109	0.132
Adult 2	0.000	0.010	0.237	0.787	0.214	0.081	0.069	0.279
Adult 3	0.000	0.000	0.000	0.090	0.786	0.016	0.014	0.527
n	125	100	97	89	14			
DE5	**λ= 1.019**		Diff. light= 4.88					
Seedl.	0.000	0.000	**0.049**	**0.209**	**0.623**	0.185	0.175	0.050
Juv.	0.349	0.440	0.105	0.000	0.000	0.137	0.140	0.111
Adult 1	0.058	0.280	0.474	0.164	0.000	0.178	0.191	0.210
Adult 2	0.000	0.020	0.355	0.650	0.325	0.329	0.333	0.283
Adult 3	0.000	0.000	0.000	0.171	0.662	0.171	0.160	0.345
n	86	50	76	140	77			

WW	**λ= 0.934**		Diff. light= 4.78					
Seedl.	0.000	0.000	**0.033**	**0.103**	**0.185**	0.068	0.052	0.054
Juv.	0.250	0.350	0.116	0.022	0.000	0.101	0.136	0.171
Adult 1	0.036	0.450	0.646	0.326	0.190	0.457	0.529	0.222
Adult 2	0.000	0.000	0.156	0.580	0.381	0.329	0.259	0.271
Adult 3	0.000	0.000	0.000	0.051	0.381	0.044	0.024	0.281
n	28	20	147	138	21			
SF	**λ= 0.951**		Diff. light= 3.52					
Seedl.	0.000	0.000	**0.014**	**0.093**	**0.192**	0.107	0.100	0.019
Juv.	0.130	0.188	0.087	0.000	0.000	0.032	0.037	0.142
Adult 1	0.000	0.375	0.500	0.116	0.061	0.158	0.172	0.183
Adult 2	0.000	0.125	0.196	0.636	0.304	0.388	0.401	0.318
Adult 3	0.000	0.000	0.022	0.231	0.617	0.315	0.289	0.336
n	23	16	46	121	115			
DE3	**λ= 0.879**		Diff. light= 1.87					
Seedl.	0.000	0.000	**0.019**	**0.185**	**0.521**	0.197	0.137	0.008
Juv.	0.088	0.400	0.127	0.015	0.000	0.066	0.117	0.076
Adult 1	0.000	0.200	0.549	0.219	0.046	0.213	0.308	0.183
Adult 2	0.000	0.000	0.127	0.657	0.356	0.355	0.337	0.304
Adult 3	0.000	0.000	0.028	0.058	0.598	0.169	0.101	0.429
n	34	25	71	137	87			
DE4	**λ= 0.933**		Diff. light= 2.09					
Seedl.	0.000	0.000	**0.016**	**0.044**	**0.155**	0.089	0.073	0.010
Juv.	0.152	0.231	0.056	0.025	0.000	0.094	0.042	0.040
Adult 1	0.019	0.154	0.481	0.086	0.032	0.155	0.127	0.183
Adult 2	0.000	0.000	0.222	0.691	0.287	0.368	0.465	0.361
Adult 3	0.000	0.000	0.000	0.173	0.660	0.294	0.293	0.406
n	105	13	54	81	94			

Table 3.8 Comparison of the 1993-94 empirical and mechanistic fecundities for each adult category.

		Adult 1	Adult 2	Adult 3	λ
DE1	Emp.	1.041	3.509		1.294
	Mech.	3.925	13.233		1.576
DE7	Emp.	0.035	0.230	1.073	0.868
	Mech.	0.169	1.107	5.168	0.958
DE2	Emp.	0.543	6.480	18.610	1.229
	Mech.	3.398	40.532	116.394	1.561
DE5	Emp.	0.049	0.209	0.623	1.019
	Mech.	0.415	1.770	5.264	1.195
WW	Emp.	0.033	0.103	0.185	0.934
	Mech.	0.252	0.783	1.404	0.999
SF	Emp.	0.014	0.093	0.192	0.951
	Mech.	0.051	0.339	0.698	0.969
DE3	Emp.	0.019	0.185	0.521	0.879
	Mech.	0.189	1.843	5.199	0.912
DE4	Emp.	0.016	0.044	0.155	0.933
	Mech.	0.143	0.864	1.422	0.957

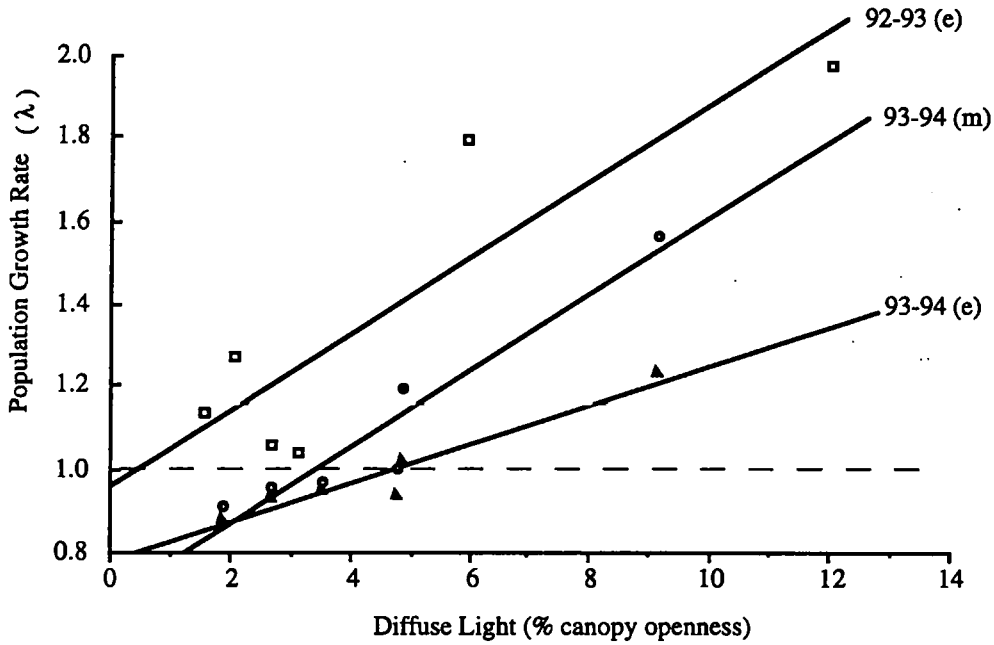
- Population Growth Rate

In general, high λ were obtained in populations in brighter patches, whereas lower λ were observed in populations under relatively darker conditions. Fig. 3.3 shows that the light environment had a strong, significant effect on population growth rate for the two periods studied. The general pattern of the relationship between λ and light was similar for the two periods studied and for both ways of calculating the fecundity elements.

Some populations were not taken into account in the linear regressions shown in Fig 3.3 because their λ were strongly affected by factors other than light. The population in the grassland (DE1) was excluded from the three regressions because its growth rate must be limited by intense competition with other species in this habitat. WW was excluded from the regression for the period 1992-93, as it showed an unusual low λ given by high mortality of adults and low reproduction due to deer over-grazing, and low recruitment due to extremely

high capsule harvest by rodents. Finally, DE7 was excluded from the 1993-94 regression because a slug plague increased mortality of adults and decreased seedling establishment, resulting in an extremely low λ.

Figure 3.3 Relationship between population growth rate (λ) and diffuse light for six *P. vulgaris* populations during the periods 1992-93 (squares) and 1993-94 (triangles). For the latter period, λ was also calculated using the mechanistic (m - circles), as opposed to the empirical (e) approach to calculate the fecundities. Diffuse light averages for summer 92 and 93 were used to plot the λ values obtained for 92-93 and the 93-94, respectively. The three regressions are statistically significant: for 92-93 (e) R^2= 0.792, d.f. = 4, p=0.01; for 93-94 (m) R^2=0.912, d.f.= 4, p=0.003; and for 93-94 (e) R^2= 0.918, d.f.= 4, p=0.002.



The differences between the λ for the two periods studied was also determined by yearly variations in mortality (Fig. 3.4). Only four populations along the light gradient are shown in the histograms in Fig. 3.4 to facilitate visual comparison. Mortality was higher in 1993-94 than in 1992-93, and darker patches (DE3 and SF) generally showed higher mortality than brighter patches (DE2 and DE5). Mortality risk decreased with increasing plant size in both periods.

Figure 3.4 Mortality recorded in the different stage categories in four populations during the periods 1992-93 and 1993-94.

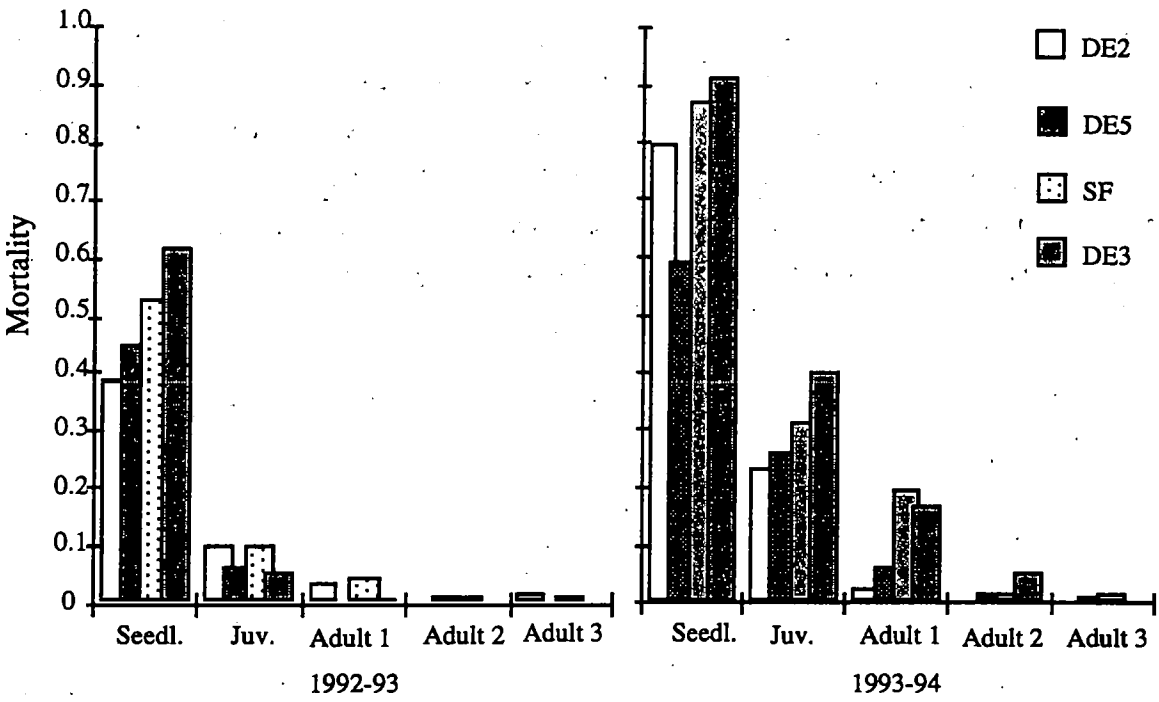
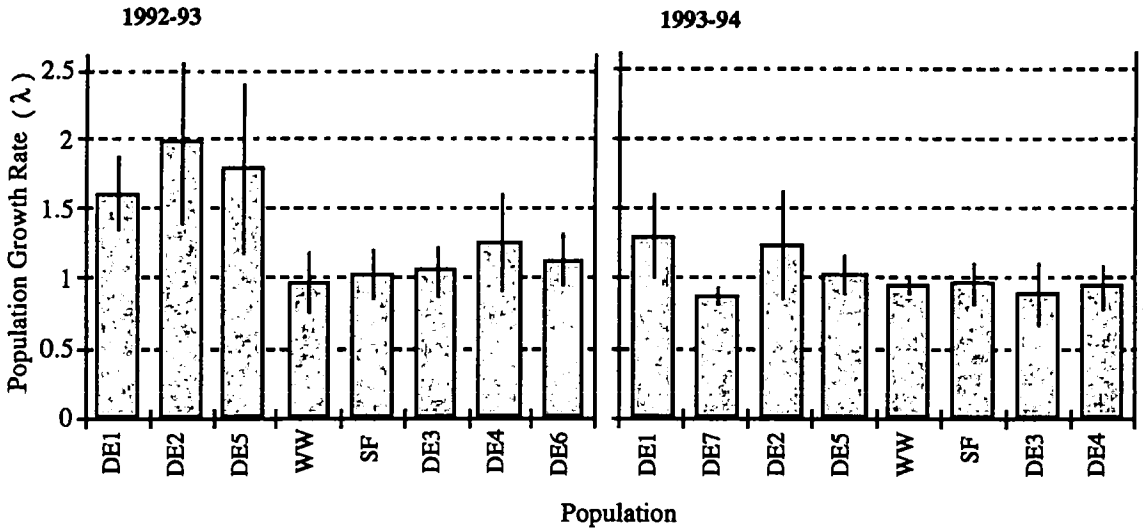


Fig. 3.5 shows the λ values obtained for the eight populations studied during both periods, together with their approximate confidence intervals at 95%. The λ of any two populations were considered to be statistically indistinguishable if the λ of one population fell within the confidence interval of the other. In 1992-93 the three populations under brighter conditions (DE1, DE2 and DE5) showed a significantly higher λ than the populations under darker conditions, with the only exception of DE4 that did not differ significantly from DE5.

For the 1993-94 period, most λ values did not differ significantly from each other, apart from DE1 *vs.* DE7 and DE1 *vs.* WW. Only DE7 and WW were significantly lower than unity. Comparing between years, populations DE1, DE2 and DE5 had significantly different λ in both periods analysed. In general, lower λ values had narrower confidence intervals.

Figure 3.5 Population growth rate (λ) with approximate 95% confidence intervals (± 2σ) for the eight populations studied during 1992-93 and 1993-94. Populations are arranged from left to right in order of decreasing diffuse light.



Although the confidence intervals for λ were wide, suggesting that there were little demographic differences between the populations studied, the log-linear analysis of entire transition matrices indicated that the effect of population and of year were both significant ($p<0.05$). Moreover, both factors interact in their effect on the fate of individuals, conditional on their initial category, i.e., the explanatory factors (year, patch, and initial category) were not independent of each other (Appendix B.1b). In such cases, Sokal and Rohlf (1981) recommend looking at the interaction between two of the factors within each level of a third one. Therefore, I tested the effect of initial category and patch on the fate of individuals for each of the two periods studied (1992-93 and 1993-94), as well as the effect of year and patch on the fate of individuals within each initial category.

The log-linear analyses performed with the transition matrices of each period revealed that both the initial category and the patch had a significant effect on the fate of individuals in both years ($p<0.05$). However, the interaction of these two factors was statistically significant only for the 1993-94 matrices (Appendix B.1c).

The log-linear analysis testing the effect of patch and year on the fate of individuals from each initial category showed that both factors had a significant effect on fate for all initial categories. However, year and patch significantly interacted in their effect on fate only in individuals coming from categories Adult 1 and Adult 2, reflecting yearly differences in the effect of patch on the fate of individuals in those categories (Appendix B.1d).

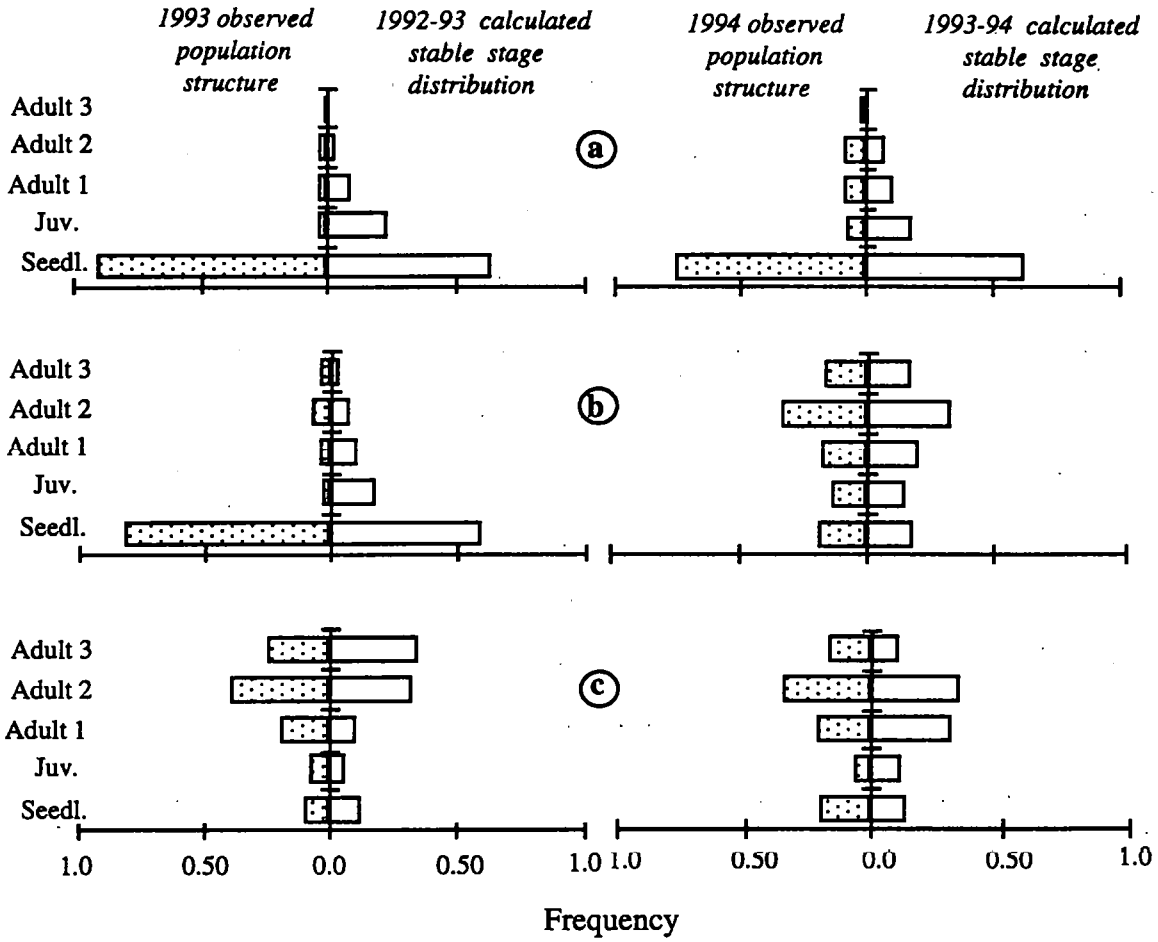
- Population Structure and Stable Stage Distributions

The population structures recorded in the 1993 and 1994 sampling dates are given in terms of the relative frequency of individuals in the different stage categories in Table 3.7. The calculated stable stage distributions (dominant right eigen-vectors of the matrices) are given in the next column of the table. The log likelihood ratio used to compare observed *vs.* calculated stable stage distributions indicates that the observed population structures significantly differed from the calculated stable distribution in most cases (Appendix B.2). The only two exceptions were in the second period studied, in the DE5 and SF populations.

Observed population structures significantly differed between years in most populations, with the exception of SF. Stable stage distributions were also significantly different for the two periods studied in all populations apart from DE2 and WW (Appendix B.2).

Fig. 3.6 shows an example of the structure of three populations for 1993 and 1994, along with the calculated stable stage distributions for 1992-93 and 1993-94. Only three populations along the light gradient were included to facilitate visual comparison. The log-linear analysis performed to test the effect of patch and year indicated that both factors, as well as the interaction between them, significantly affected the frequency of individuals per category (Appendix B.1a). In general, the relative frequency of large individuals increased with decreasing light availability.

Figure 3.6 Population structures recorded in 1993 and 1994 and stable stage distributions calculated from the projection matrices of the periods 1992-93 and 1993-94 for a) a population in a large gap (DE2), b) a population in a small gap (DE5), and c) a population under closed canopy conditions (DE3).



- Reproductive Values

The reproductive values obtained from the analysis of projection matrices are given in the last column of Table 3.7. As with stable stage distributions, they have been normalised to unity. Note the positive correlation between reproductive value and plant size (as given by stage category). For the period 1992-93, the seedlings of populations under brighter conditions (DE1, DE2, DE5) had particularly low reproductive values. The three reproductive categories (adult 1, 2 and 3) showed quite similar reproductive values in patches in darker conditions, whereas in populations under brighter conditions the difference between categories was more noticeable. This pattern was also present, though not as clear, in the results of the 1993-94 period.

3.3.3 Sensitivity and Elasticity Analysis

Table 3.9 show the sensitivity and elasticity matrices for 1992-93 and 1993-94. The total sensitivity and the sensitivity index (square root of the total sensitivity) for each matrix are also given, as well as the corresponding λ value. In the populations in brighter patches the highest sensitivities often corresponded to growth transitions from young to adult stages. In some cases, entries that implied fast growth (by skipping one category, e.g., seedling to adult 1, or juvenile to adult 2) were particularly high. For populations in darker patches high sensitivities corresponded to the growth of adults to larger categories or their persistence in the same category (i.e., in the bottom, right-hand corner of the matrix). The highest sensitivity values were almost always less than 25% of the total sensitivity, and this percentage decreased in populations under darker conditions. λ was less sensitive, in most cases, to fecundity elements, especially for populations in brighter patches. The lowest sensitivity value was almost always below 1% of the total sensitivity. These patterns were similar for both periods studied.

The sensitivity index measures the sensitivity of λ to changes in the entire life cycle (Caswell 1978). In this study sensitivity indices varied from 1.615 to 2.695 and were quite similar between years, though in most cases they were smaller in 1993-94. In the first year the woodland populations under brighter conditions (DE2, DE5 and WW) showed higher sensitivity indices than the populations under closed canopy conditions. However, this pattern was not maintained in 1993-94.

Elasticities represent the proportional contribution of each entry of the transition matrix to population growth rate. Entries with higher elasticity rarely coincided with those of higher sensitivity (Table 3.9). In general, the elasticity of fecundity elements was low; the lowest elasticity value of 8 out of the 16 matrices in Table 3.9 was a fecundity entry. As a general trend, populations in brighter patches showed higher fecundity elasticities.

Table 3.9 Sensitivity and Elasticity matrices for eight populations of *P. vulgaris* for the period 1992-93 (a) and 1993-94 (b). The two highest values are bold and the smallest value is underlined in each matrix.

Table 3.9a	**Sensitivity**					**Elasticity**				
	Seedl.	Juv.	Adult 1	Adult 2	Adult 3	Seedl.	Juv.	Adult 1	Adult 2	Adult 3
DE1	λ=1.622	Tot.S = 2.914		S.index =1.707						
Seedl.	0	0	0.093	0.007		0	0	0.174	0.024	
Juv.	0.395	0.296	0.186	0		0.198	0.093	0.005	0	
Adult 1	0	**0.727**	0.456	0.034		0	**0.203**	**0.242**	0.012	
Adult 2	0	0	**0.671**	0.049		0	0	0.036	0.013	
DE2	λ=1.976	Tot.S = 7.261		S.index =2.695						
Seedl.	0	0	0.029	0.011	0.001	0	0	0.066	0.127	0.015
Juv.	0.632	0.240	0.089	0	0	**0.188**	0.051	0.001	0	0
Adult 1	**1.946**	0.740	0.275	0.102	0	0.020	**0.170**	0.078	0.006	0
Adult 2	0	**1.831**	0.679	0.252	0.015	0	0.019	0.129	0.099	0.005
Adult 3	0	0	0	0.395	0.024	0	0	0	0.020	0.004
DE5	λ=1.794	Tot.S = 5.192		S.index =2.278						
Seedl.	0	0	0.038	0.028	0.011	0	0	0.045	0.087	0.079
Juv.	0.550	0.169	0.098	0	0	**0.136**	0.031	0.002	0	0
Adult 1	**1.208**	0.370	0.216	0.163	0	0.075	0.101	0.037	0.002	0
Adult 2	0	**0.566**	0.330	0.249	0.095	0	0.036	**0.105**	0.091	0.017
Adult 3	0	0	0.539	0.407	0.155	0	0	0.027	0.069	0.059
WW	λ=0.974	Tot.S = 4.445		S.index =2.108						
Seedl.	0	0	0.251	0.174	0.014	0	0	0.006	0.016	0.004
Juv.	0.045	0.054	0.411	0.284	0	0.020	0.015	0.017	0.002	0
Adult 1	0.052	0.063	0.480	0.332	0	0.008	0.035	**0.326**	0.1113	0
Adult 2	0	0.076	**0.579**	0.401	0.032	0	0.003	0.125	**0.255**	0.018
Adult 3	0	0	**0.685**	0.474	0.038	0	0	0.006	0.016	0.016
SF	λ=1.035	Tot.S = 3.285		S.index =1.812						
Seedl.	0	0	0.033	0.112	0.188	0	0	0.001	0.007	0.034
Juv.	0.087	0.032	0	0	0	0.025	0.008	0	0	0
Adult 1	0.100	0.037	0.080	0.267	0.450	0.017	0.013	0.029	0.015	0.005
Adult 2	0	0.041	0.089	0.297	**0.500**	0	0.012	0.039	**0.163**	0.082
Adult 3	0	0	0.097	0.326	**0.549**	0	0	0.010	0.112	**0.427**
DE3	λ=1.055	Tot.S = 3.327		S.index =1.824						
Seedl.	0	0	0.038	0.115	0.122	0	0	0.001	0.016	0.027
Juv.	0.120	0.067	0.104	0	0	0.044	0.019	0.004	0	0
Adult 1	0	0.072	0.111	0.339	0.358	0	0.044	0.040	0.012	0.016
Adult 2	0	0.079	0.121	0.371	**0.391**	0	0.004	0.061	**0.220**	0.086
Adult 3	0	0	0.126	0.386	**0.407**	0	0	0.005	0.123	**0.279**
DE4	λ=1.267	Tot.S = 3.464		S.index =1.861						
Seedl.	0	0	0.091	0.089	0.113	0	0	0.024	0.036	0.091
Juv.	0.272	0.055	0.163	0	0	0.043	0.007	0.005	0	0
Adult 1	**0.344**	0.070	0.206	0.202	0	**0.108**	0.026	0.059	0.013	0
Adult 2	0	0.081	0.238	0.233	0.298	0	0.018	0.066	0.088	0.062
Adult 3	0	0.096	0.283	0.277	**0.353**	0	0.004	0.052	0.098	**0.200**
DE6	λ=1.133	Tot.S = 3.719		S.index =1.928						
Seedl.	0	0	0.109	0.117	0.096	0	0	0.012	0.031	0.053
Juv.	0.153	0.083	0.176	0.188	0	0.051	0.029	0.001	0.002	0
Adult 1	0.201	0.110	0.232	0.248	0.204	0.044	0.054	0.094	0.036	0.003
Adult 2	0	0	0.272	0.291	0.240	0	0	0.095	**0.151**	0.045
Adult 3	0	0	**0.339**	**0.362**	0.298	0	0	0.030	0.071	**0.198**

Table 3.9b	**Sensitivity**					**Elasticity**				
	Seedl.	Juv.	Adult 1	Adult 2	Adult 3	Seedl.	Juv.	Adult 1	Adult 2	Adult 3
DE1	λ=1.294	Tot.S = 3.687		S.index =1.920						
Seedl.	0	0	0.049	0.032		0	0	0.039	0.087	
Juv.	0.317	0.249	0.123	0		0.126	0.120	0.003	0	
Adult 1	0	**0.624**	0.308	0.201		0	0.121	**0.161**	0.026	
Adult 2	0	**0.983**	0.485	0.316		0	0.008	0.104	**0.204**	
DE7	λ=0.868	Tot.S = 3.394		S.index =1.842						
Seedl.	0	0	0.106	0.073	0.012	0	0	0.004	0.019	0.015
Juv.	0.060	0.093	0.168	0.115	0	0.031	0.036	0.018	0.008	0
Adult 1	0.130	0.200	0.361	0.247	0.041	0.008	0.056	**0.206**	0.085	0.006
Adult 2	0	0	**0.592**	0.405	0.067	0	0	0.133	**0.234**	0.038
Adult 3	0	0	0	**0.622**	0.102	0	0	0	0.060	0.043
DE2	λ=1.229	Tot.S = 5.878		S.index =2.424						
Seedl.	0	0	0.018	0.011	0.002	0	0	0.008	0.060	0.035
Juv.	0.578	0.168	0.100	0.064	0	0.094	0.067	0.007	0.001	0
Adult 1	**1.474**	0.428	0.255	0.162	0	0.009	0.094	**0.137**	0.015	0
Adult 2	0	**0.900**	0.537	0.342	0.069	0	0.007	0.104	**0.218**	0.012
Adult 3	0	0	0	0.646	0.131	0	0	0	0.047	0.084
DE5	λ=1.019	Tot.S = 3.132		S.index =1.770						
Seedl.	0	0	0.045	0.078	0.037	0	0	0.002	0.016	0.023
Juv.	0.091	0.073	0.100	0	0	0.031	0.032	0.010	0	0
Adult 1	0.172	0.138	0.188	0.327	0	0.010	0.038	0.087	0.053	0
Adult 2	0	0.186	0.252	**0.439**	0.211	0	0.004	0.088	**0.280**	0.067
Adult 3	0	0	0	**0.537**	0.258	0	0	0	0.090	**0.168**
WW	λ=0.934	Tot.S = 3.322		S.index =1.823						
Seedl.	0	0	0.130	0.064	0.006	0	0	0.005	0.007	0.001
Juv.	0.040	0.106	0.410	0.201	0	0.011	0.039	0.051	0.005	0
Adult 1	0.052	0.138	**0.533**	0.261	0.024	0.002	0.066	**0.369**	0.091	0.005
Adult 2	0	0	**0.650**	0.318	0.029	0	0	0.109	**0.197**	0.012
Adult 3	0	0	0	0.330	0.030	0	0	0	0.018	0.012
SF	λ=0.951	Tot.S = 3.039		S.index =1.743						
Seedl.	0	0	0.013	0.029	0.021	0	0	0.0002	0.003	0.004
Juv.	0.054	0.020	0.093	0	0	0.007	0.004	0.008	0	0
Adult 1	0	0.025	0.120	0.278	0.200	0	0.010	0.063	0.034	0.013
Adult 2	0	0.044	0.209	**0.486**	0.350	0	0.006	0.043	**0.325**	0.112
Adult 3	0	0	0.219	**0.510**	0.368	0	0	0.005	0.124	**0.239**
DE3	λ=0.879	Tot.S = 3.670		S.index =1.916						
Seedl.	0	0	0.011	0.012	0.003	0	0	0.0002	0.003	0.002
Juv.	0.049	0.042	0.111	0.121	0	0.005	0.019	0.016	0.002	0
Adult 1	0	0.101	0.266	0.291	0.087	0	0.023	**0.166**	0.072	0.005
Adult 2	0	0	0.442	0.483	0.144	0	0	0.064	**0.361**	0.058
Adult 3	0	0	**0.623**	**0.681**	0.203	0	0	0.020	0.045	0.138
DE4	l=0.933	Tot.S = 2.610		S.index =1.615						
Seedl.	0	0	0.004	0.015	0.010	0	0	0.0001	0.001	0.002
Juv.	0.009	0.005	0.016	0.059	0	0.001	0.001	0.001	0.001	0
Adult 1	0.042	0.025	0.074	0.272	0.172	0.001	0.004	0.038	0.025	0.006
Adult 2	0	0	0.047	**0.537**	0.339	0	0	0.035	**0.398**	0.104
Adult 3	0	0	0	**0.603**	0.381	0	0	0	0.112	**0.269**

High elasticity values tend to concentrate in the entries that correspond to young/small individuals growing to larger categories in populations under brighter conditions (middle left-hand side of the matrices). On the other hand, for populations in darker patches high elasticities were found in the entries that correspond to large adults remaining in the same category or growing to the next one (towards the bottom, right-hand side of the matrices). This pattern was more noticeable in the 1992-93 period.

The contribution of different parts of the life cycle to population growth rate can be studied through the analysis of the elasticity values of matrix elements that correspond to different 'demographic behaviour' (van Groenendael and Slim 1988; Silvertown *et al.* 1993; van Groenendael *et al.* 1994). Total elasticities for particular elements of the life cycle can be calculated by adding together all the elasticity values involved in specific transitions. Thus, total elasticity for fecundity elements (contribution to the first category through the production of seeds), survival (remaining in the same category or shrinking to smaller categories) and growth (progressing to larger categories) can be plotted on a triangular diagram with each axis corresponding to one of these three basic elements of the life cycle graph (Silvertown *et al.* 1993).

Following this methodology I used the data in the elasticity matrices of Table 3.9 to generate a triangular diagram in which I represented each population (Fig. 3.7). Populations are concentrated on the centre and bottom part of the triangle, towards the right-hand corner. This pattern correspond to high elasticities for survival elements and low elasticities for fecundity elements. The 1992-93 distribution pattern shows higher elasticities for growth and fecundity elements and lower elasticities for survival elements relative to the one in 1993-94. This accounts for the distribution of the dots closer to the right, bottom corner of the triangle in 1993-94.

Figure 3.7 Triangular graphs of fecundity (F), survival (L) and growth (G) elasticities for the periods a) 1992-93 and b) 1993-94 for the nine populations studied. Each circle in the graphs represents a population (Dancers End populations referred to by number, and Salcey Forest and Woburn Wood populations referred as S and W, respectively).

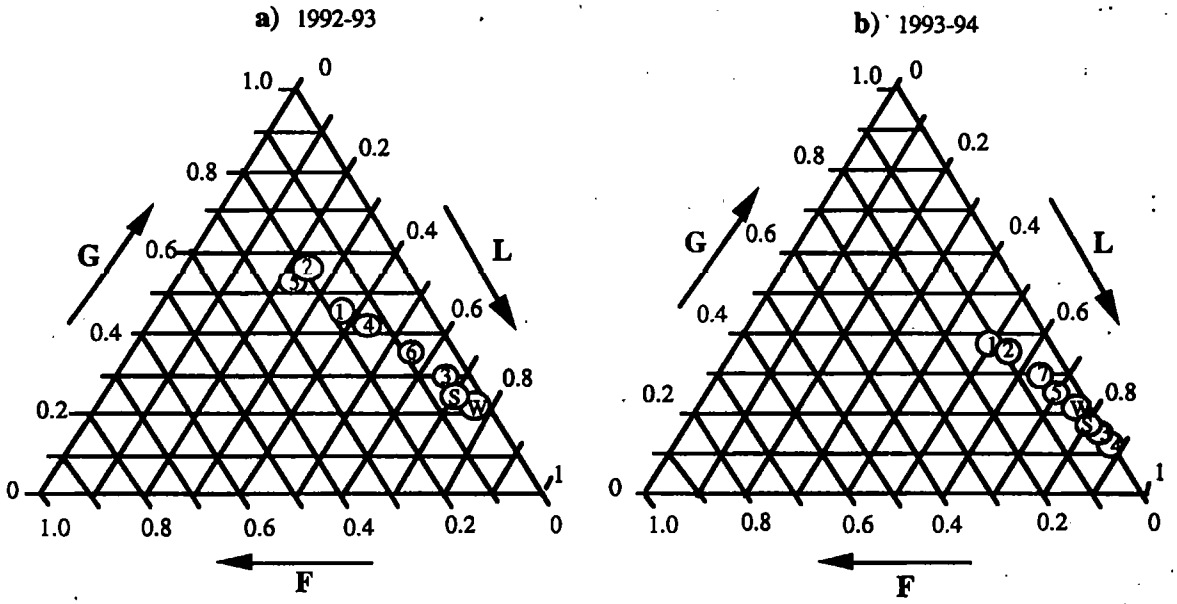
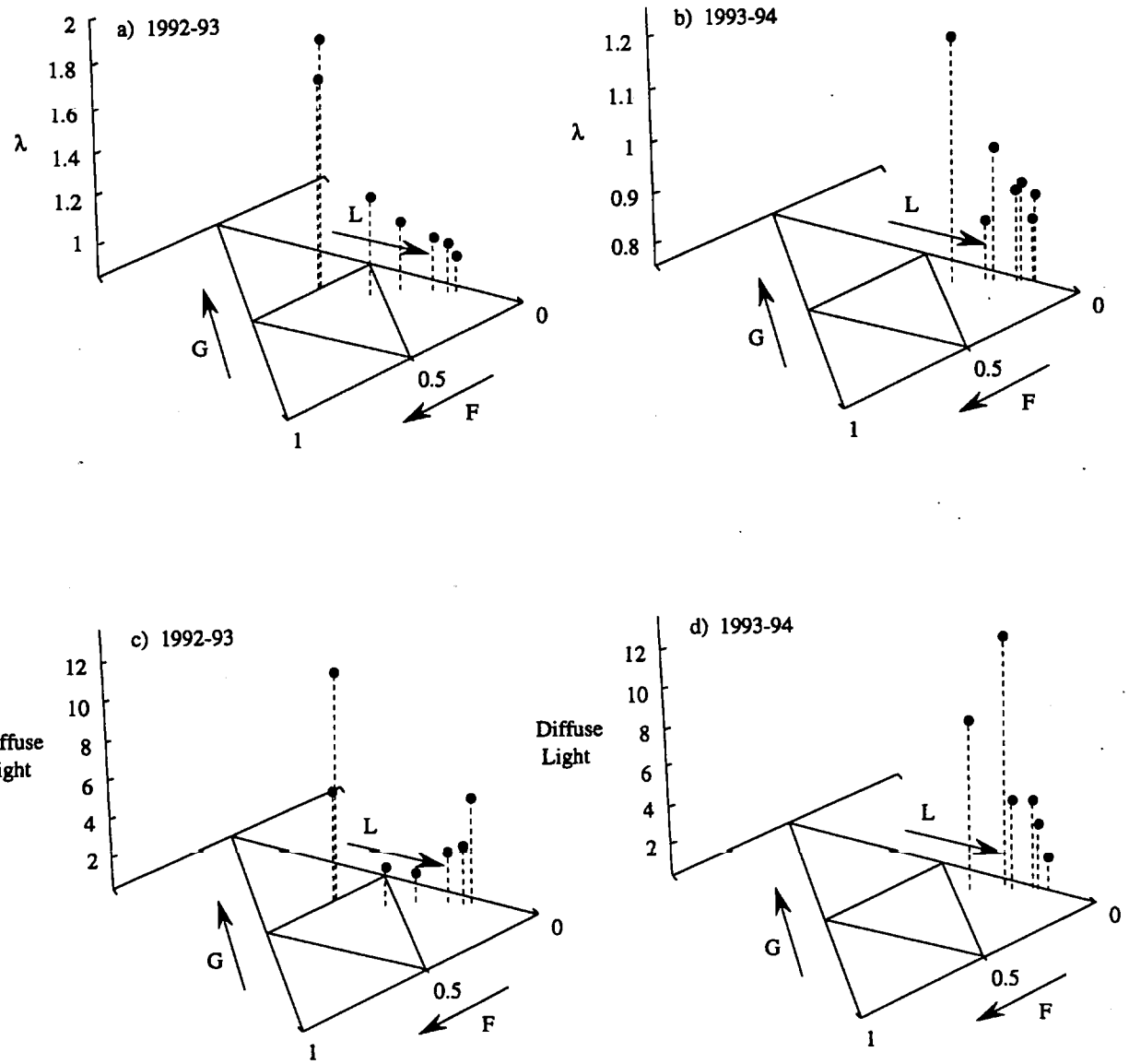


Fig. 3.8 shows three-dimensional plots of survival, fecundity and growth elasticities in relation to population growth rate (Fig. 3.8 A and B) and diffuse light (Fig. 3.8 C and D). Only the woodland populations are included in these plots (DE1 was not taken into account). Populations with higher λ values had relatively higher fecundity and growth elasticities (i.e., they fell closer to the centre of the triangle) than populations with lower λ values, which in turn, showed high survival elasticities (i.e., they fell closer to the survival axis of the triangle). This pattern was particularly clear for the 1992-93 results. In general, populations with higher diffuse light had higher fecundity and growth elasticities than populations with low diffuse light. This trend was more apparent in 1993-94. A notable exception, though, was the population in Woburn Wood for the period 1992-93 (5.6% diffuse light), which occupies the far bottom right-hand corner of the triangle despite having similar light conditions to DE5 (5.9% diffuse light), a population that fell almost in the opposite extreme of the continuum formed by all the populations.

Figure 3.8 Three-dimensional plots showing fecundity (F), survival (L) and growth (G) elasticities in relation to population growth rate, λ, (A and B) and diffuse light (C and D) in the periods 1992-93 and 1993-94 for the woodland populations studied. Note the different scales in the vertical axis between A and B. Diffuse light values (% canopy openness) correspond to average diffuse light measured in each population during summer 1992 (C) and 1993 (D).



3.4 Discussion

These results show that the demography of populations of *P. vulgaris* varied spatially according to the light conditions of the specific forest patch they occupied. This suggests that, on a longer time-scale than the one used in this study, population dynamics may change as a result of natural changes in the forest canopy. Population growth rate tends to be lower in darker patches, implying that populations decline as the canopy closes. A similar demographic behaviour was inferred for *Calathea ovandensis* (Horvitz and Schemske 1986) and for *Cynoglossum virginianum* (Cipollini *et al.* 1993). However, Horvitz and Schemske (1986) assumed that *C. ovandensis* would follow a 'non-linear slow' rate of demographic change as a result of canopy closure (as opposed to 'linear', or 'non-linear-fast'), whereas the actual rate of demographic change in *P. vulgaris* (as measured by λ in relation to light conditions) was satisfactorily described by a linear function. Accordingly, *P. vulgaris* populations under completely closed canopy conditions may show negative growth rates, as shown by the results of this chapter. This supports the idea that local populations can be led to extinction as a result of canopy closure. The persistence of this kind of gap-dependent species in a forest may then depend on the maintenance of metapopulations through a balance between colonisations and extinctions. Although extinction of natural populations could also occur as a result of stochastic events, in this case it appears to be mainly a deterministic processes caused by canopy closure.

Most of the λ values obtained for the period 1992-93 were greater than one, indicating that even under the darkest conditions populations manage to persist. However, the λ for that particular period were slightly overestimated because population sampling was delayed in 1992 (starting in June instead of May), when most of the seedlings recorded that season were already established. Since I missed the period of typically heavy seedling mortality that occurs after germination in most plant species, the 'seedling-to-juvenile' transition was overestimated, resulting in inflated λ values for the 1992-93 period. Population sampling in

1993 and 1994 allowed a much more accurate λ estimate. In fact, the 1993-94 λ values were smaller than the ones obtained for 1992-93, with only three of them exceeding unity.

The differences in the λ values for the two periods studied were not only due to overestimating seedling survival from 1992 to 1993. In addition, mortality was higher during 1993-94 in most populations (Fig. 3.4), particularly in the smaller categories, consistent with the results reported for other woodland herbs (Cook 1980; Bierzychudek 1982b). Also, fecundities were higher in 1992-93 than in 1993-94 due to high flower (and presumably seed) production in 1992 and the consequent high seedling emergence in 1993. These two events were noticeable in the field, particularly in some of the Dancers End populations, and had a strong effect on population growth rate. Other authors have reported that capsule production (and hence seed set) in natural populations of *P. vulgaris* vary greatly from year to year, apparently related to pollinator availability (Piper *et al.* 1984; Boyd *et al.* 1990). The fact that fecundities varied from patch to patch along the light gradient, as well as in time, suggests that there may also be light-related differences in pollinator abundance within forest patches.

For the 1993-94 period fecundities were estimated using both the empirical and the mechanistic methods. For all populations and all categories considered mechanistic fecundities were consistently higher than empirical fecundities. One explanation for this discrepancy is that the mechanistic method avoided any potential effect of pre-dispersal seed loss on final fecundity, because seedling emergence from seeds sown directly into the soil was taken into account to calculate fecundities. Seed removal by ants and rodents in *P. vulgaris* occurs at a high rate in the populations studied. Some populations in Dancers End may lose between 50 and 60% of their seeds due to ant and rodent foraging (Valverde and Silvertown, in press, Appendix A). The differences in the results of the two methods used to calculate fecundity offers a further insight into the potential effects of seed removal on the growth rate of natural populations under various light conditions.

Although population growth rate varied in time and space, as seems to be common in other forest herbs (Barkham 1980; Bierzychudek 1982b; Horvitz and Schemske 1995), the approximate confidence intervals for λ were wide with only a few cases showing significant differences between populations and/or years. Alvarez-Buylla and Slatkin (1993, 1994) pointed out that the analytical method for estimating λ's confidence intervals was reliable if the coefficients of variations for entries of the matrix to which λ is very sensitive were sufficiently low (< 50%). According to this method, the confidence intervals for λ are largely dependant on the sensitivities of matrix entries: those entries with a high sensitivity will contribute large values to the overall variance of λ (Caswell 1989). Such high sensitivities often corresponded to fast growth (skipping categories from one year to the next - see Table 3.9) consistent with the results of other authors (Enright and Ogden 1979; Bierzychudek 1982a; Horvitz and Schemske 1995). However, most of these transitions showed low frequencies and were calculated from few individuals, which resulted in high coefficients of variation. Thus, the coefficients of variation of high sensitivity entries were sometimes well above 50%; the confidence intervals for λ reported here should thus be treated with caution. Nevertheless, some indication of the uncertainty associated with the calculation of λ is always more illustrative than reporting only the mere λ values (Caswell 1989).

Given the wide confidence intervals for λ, few statistically significant differences between λ values were found. However, the log-linear analysis of transition matrices revealed that both patch and year (as well as the interaction of both factors) had a significant effect on the fate of individuals. Using a similar methodology, Ehrlen (1995) also found that in a perennial forest herb, *Lathyrus vernus*, site and year had a significant effect on the demographic fate of individuals, even though no significant differences in the λ were found between years. Thus, differences in population dynamics in various forest patches and in different periods of time are detectable in other demographic features in addition to the variation in population growth rate.

The structure of the *P. vulgaris* populations I studied was not independent of patch and year (Appendix B.1a). Smaller/younger individuals had higher frequencies in brighter patches than in populations under completely closed canopy conditions. The change in population structure from brighter to darker patches suggests that seedling recruitment is high during the phase of population establishment following the opening of gaps, but as the canopy closes seedling emergence decreases and populations persist largely due to the survival of established individuals. This is also a common phenomenon among other forest understory herbs (Pitelka *et al.* 1985; Barkham 1992b; Cipollini *et al.* 1993; Hara and Wakahara 1994; Horvitz and Schemske 1994).

Most of the populations studied were not quite at equilibrium. Although λ values were sometimes close to unity, their population structures were generally significantly different from the stable stage distribution. Natural populations are often not at their stable stage distribution (Caswell 1989). However, the main demographic assumption behind the concept of stable stage distribution is that the environment is constant, thus it is not surprising that *P. vulgaris* populations growing in a permanently changing environment have population structures that differ from those expected at equilibrium. There is no such thing as 'equilibrium' for a population embedded in a system of constantly changing conditions determined by the dynamics of the canopy.

Although the results presented in this chapter are based on a period of two growth seasons, the analysis of different populations along a light gradient suggests that the demography of gap-dependent species such as *P. vulgaris*, changes from year to year not only due to the effect of random or climatic events, but also as a result of canopy closure (Horvitz and Schemske 1986; Alvarez-Buylla and García-Barrios 1991). Analysis of the elasticities shows that this results in a directional change in demographic parameters. Different elements of the life cycle varied in their contribution to λ between lighter and darker patches. Fecundity and growth had a larger contribution to λ in populations under brighter conditions, and survival became more important in populations under the closed canopy.

The region of the demographic triangle in which *P. vulgaris* populations in brighter patches were concentrated (Fig. 3.8) slightly coincides with the pattern found by Silvertown *et al.* (1993) for iteroparous herbs of open habitats. On the other hand, populations in darker patches were closer to the survival axis, which is the case of most of the perennial forest herbs analysed by Silvertown *et al.* (1993).

In *Cynoglossum virginianum*, another temperate forest herb, Cipollini *et al.* (1993) found that the contribution of the seed-to-seedling transition to the value of λ was more important in populations established in new gaps than in populations under closed canopy conditions. Silvertown and Franco (1993) found that the contribution of fecundity to population growth rate in several species was higher during the early stages of colonisation than later in the successional process. This suggest that the trends observed in the demographic changes of *P. vulgaris* in response to canopy closure are not unique and stresses the importance of studying the variation in the dynamics of plant populations across the range of habitat patches in which they naturally occur.

Chapter 4. Forest Structure and Canopy Dynamics

4.1 Introduction

In Chapter 3 I illustrated the effect of the environmental change resulting from canopy closure on the dynamics of local population of *Primula vulgaris*. Populations under completely closed canopy conditions may show negative growth rates, suggesting that local populations may eventually go extinct. The demography of local populations is one of the elements to consider in the dynamics of a metapopulation. In this chapter I turn towards the system in which local populations are embedded: the forest as a whole with its own dynamics processes in time and space.

The importance of patch dynamics in the maintenance of habitat heterogeneity and hence community diversity in different types of ecosystems has been widely documented (Doyle 1981; Brokaw 1985a, 1985b; Martínez-Ramos *et al.* 1985; Pickett and White 1985; Runkle and Yetter 1987; Whitmore 1989; Alvarez-Buylla and García-Barrios 1991; O'Connor 1991; Lertzman 1992; Veblen *et al.* 1994; Wu and Levin 1994). The disturbance/re-growth cycle involved in patch dynamics is of ecological interest in itself, but also because it is linked with many other ecological processes occurring at different spatial and temporal scales.

There are several ecological processes that occur at the level of the canopy and may affect *P. vulgaris* metapopulation dynamics. The rate at which the canopy closes after gap formation will determine the window of time during which *P. vulgaris* populations may show positive growth rates, which will, in turn, determine their vulnerability to extinction. On the other hand, gap formation rate will affect the likelihood of new local populations becoming

established. This chapter addresses these issues in order to explore the way in which the dynamics of the forest as a whole imposes times and rates on metapopulation processes. Of particular interest are the rate of gap opening and closure, and the effect of these processes on forest structure. In this chapter I develop a model based on empirical data on canopy closure in order to describe the dynamics of the forest mosaic.

4.2 Methods

4.2.1 Hemispherical Photography and Light Measurement

Hemispherical photographs were used to characterize the light environment and to evaluate the rate of change of canopy cover for each population studied. This technique involves the use of a hemispherical lens (180°, "fish-eye") to photograph the forest canopy from below. It has several advantages over other methods of evaluating of the light conditions beneath forest canopies, the main one being that it is an instantaneous measurement that provides a quantification of the light conditions integrated over long periods of time (Anderson 1964; Mitchell and Whitmore 1993).

Each population was photographed in August of 1992, 1993 and 1994. To ensure that the camera was placed in the same points each year, the plastic pipes of the permanent quadrats were used as a reference (see Chapter 3). The camera was set on a tripod at 50cm above the ground level, with the lens pointing vertically towards the canopy and the top of the camera pointing towards the north. A spirit level was used to ensure that the lens was horizontal. Photographs were taken with an Olympus Auto-fisheye lens (1:2.8, f=8mm) using a black and white, high-contrast film (Ilford PANF, ASA 50) and mostly during overcast days in order to avoid unevenness in the brightness of the pictures.

The computer program Image 1.42 (Macintosh) was used to capture the hemispherical images through a video camera using the negatives. Contrast and brightness were adjusted over all or part of the image by comparing the captured images with contact prints. In some cases, drawing commands were used to modify the image for clarity, e.g. to emphasize the distinction between a dark cloud and the vegetation. This procedure may introduce errors. However, human interpretation is preferable to arbitrary standards as these differences can sometimes be too subtle for the computer's resolution (Chazdon and Field 1987).

The resultant image was transformed into a MacDraw picture in which closed areas were black and open areas were white (a one-bit screen map). These standardized images were then analysed to obtain the desired light measurements using the program Solarcalc 5.41 (Macintosh II), developed by Chazdon and Field (1987). The key parameter obtained was diffuse light (or diffuse site factor, measured as the percentage of open sky in the photograph - Anderson 1964; Mitchell and Whitmore 1993). The mean diffuse light of 7 to 15 photographs per year was used to describe the light conditions in each population.

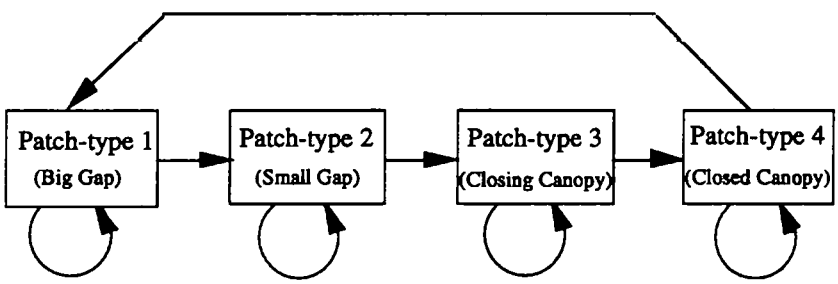
4.2.2 Canopy Dynamics Model

Other authors have described patch dynamics using models which subdivide forest patches into types according to variables ultimately related to their successional stage along the forest regeneration cycle, i.e. light conditions, age since last disturbance, and/or gap size. Some of these studies have derived models from a generalized Lefkovitch projection matrix incorporating forest dynamics as a linear Markov-chain process of forest succession following disturbance caused by tree-fall gaps (Horvitz and Schemske 1986; Martinez-Ramos *et al.* 1989; Alvarez-Buylla and García-Barrios 1991; Cipollini *et al.* 1993, 1994; Alvarez-Buylla 1994). Here I used a similar approach to describe the equivalent process in the forest at Dancers End reserve.

I considered the existence of different patch types, defined according to light conditions, along the range of forest patches usually occupied by *P. vulgaris* (Fig. 4.1a). Two different approaches to patch-type categorisation were considered to test the effect of this factor on the results (see below, section 4.3.2). The model assumes that 1) each patch type may remain the same or become the next patch type as the canopy closes in one time step, and 2) type-1 patches (gaps) may be created due to natural disturbances only in type-4 patches (completely closed canopy conditions). The probability of these disturbances happening in other patch types was deemed negligible as most of the forest is composed of type-4 patches.

Figure 4.1 a) Schematic model of forest canopy dynamics. Each box represents a patch-type and the arrows indicate transitions between patch-types over one time step. b) Corresponding matrix model of canopy dynamics.

a)



b) Matrix **P**

Patch-type at time t+1 \ Patch-type at time t	1	2	3	4
1	p1,1	0	0	p1,4
2	p2,1	p2,2	0	0
3	0	p3,2	p3,3	0
4	0	0	p4,3	p4,4

This model is represented mathematically by the matrix, **P**, an *nxn* matrix, where *n* is the number of patch-types (Fig. 4.1b). Each matrix entry, $p_{i,j}$, represents the transition probability from a type-*j* patch to a type-*i* patch after one year. Let f_t be a vector representing the number of patches of each type at time t in the forest. The structure of the forest after one year can be described by the vector f_{t+1}, where

$$f_{t+1} = \mathbf{P}_{i,j} \times f_t \qquad (1)$$

Note all matrix entries are zero except the diagonal, the sub-diagonal, and the upper right entry. This latter matrix element, $p_{1,n}$, represents the probability of gap formation in closed canopy patches, i.e. the disturbance regime. Thus, the probability of closed canopy patches remaining as such, $p_{n,n}$, is given by 1 - $p_{1,n}$. Other matrix entries are calculated according to the rate of canopy closure (see below).

The right eigen-vector of matrix **P** associated with the dominant eigen-value (λ=1.000) is proportional to the distribution of patch types in the forest at equilibrium, or the 'stable patch-type distribution'.

4.3 Results

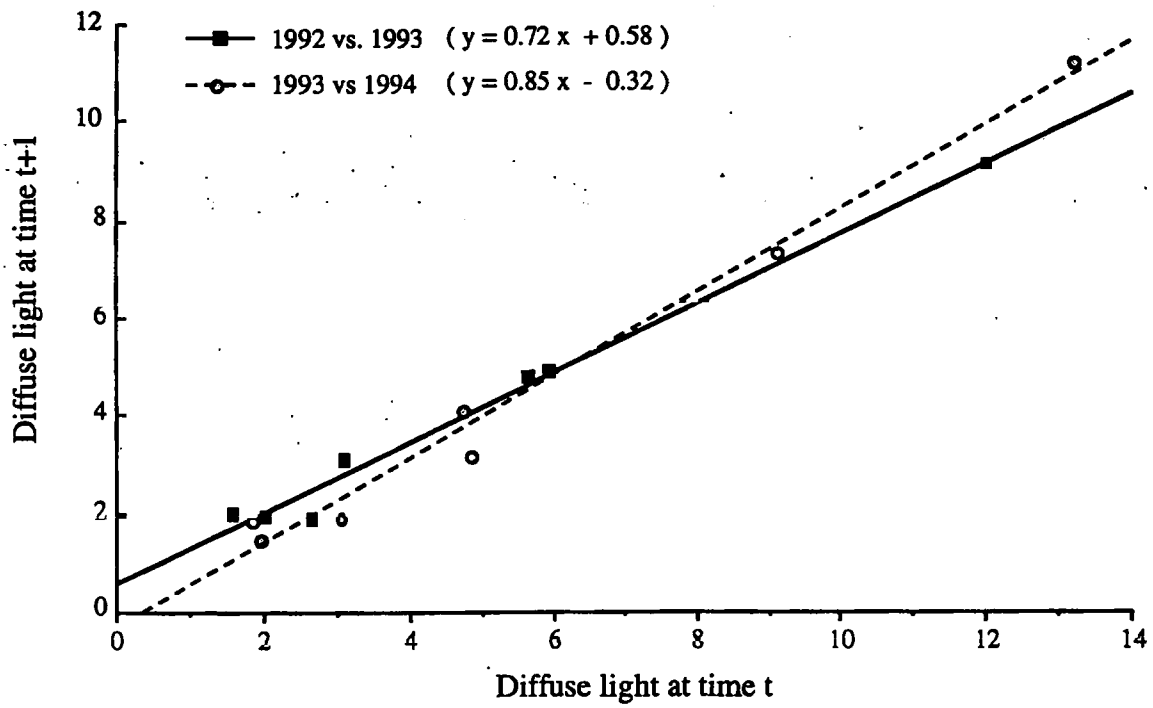
4.3.1 Canopy Closure Rate

The rate of canopy closure was estimated by comparing the mean diffuse light obtained per patch in consecutive years. Table 4.1 shows the main results of the analysis of the hemispherical photographs taken in August 1992, 1993 and 1994. The mean diffuse light per patch did change each year, and generally these changes were more noticeable in brighter patches. Both periods showed a strong linear relationship between the light conditions at times t and t+1 (Fig. 4.2).

Table 4.1 Mean diffuse light for *P. vulgaris* populations at Dancers End (DE), Woburn Wood (WW) and Salcey Forest (SF). Populations are given in order of decreasing diffuse light. Other details of these results given in Table 3.6.

Population	Diffuse light (% canopy openness)		
	1992	1993	1994
DE7	—	13.21	11.16
DE2	12.01	9.12	7.31
DE5	5.95	4.88	3.16
WW	5.65	4.78	4.05
SF	3.09	3.08	1.90
DE3	2.67	1.87	1.84
DE4	2.03	1.95	1.46
DE6	1.57	1.97	—

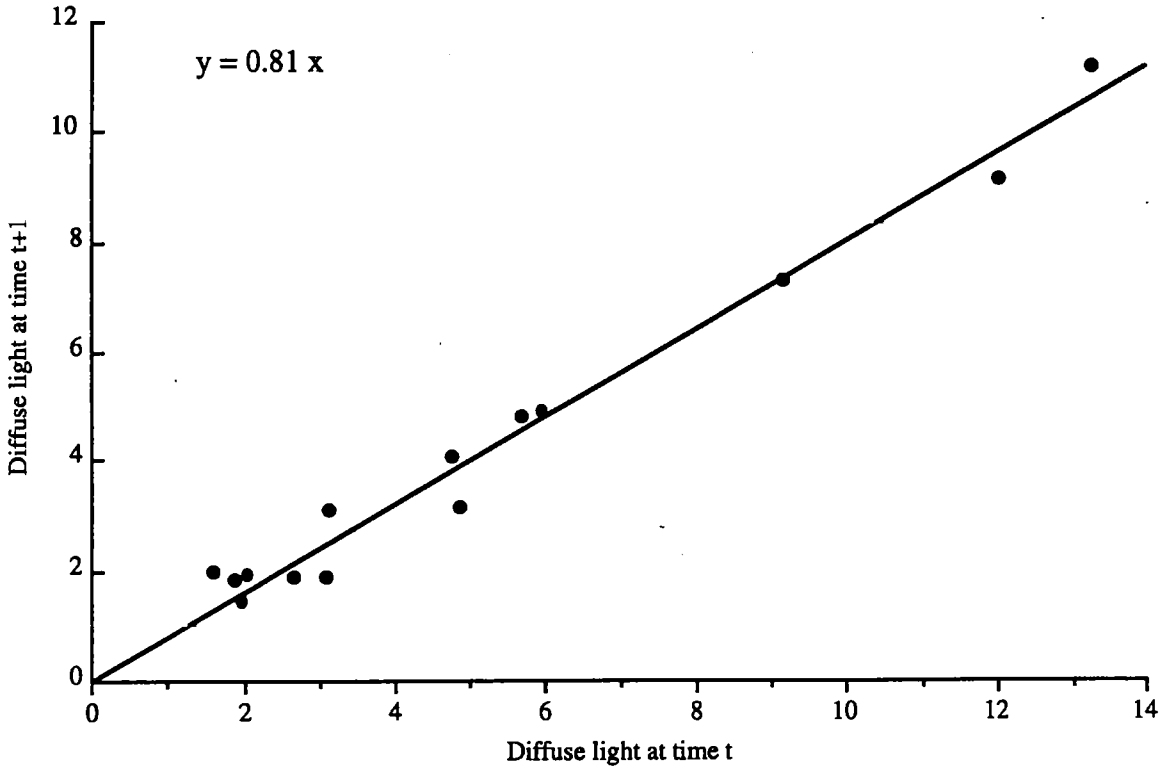
Figure 4.2 Relationship between diffuse light (given as % canopy openness) at times t and t+1 for 1992-1993 and the 1993-1994 data sets. Coefficients of the linear regression are given in the upper left hand corner. In both cases $R^2 = 0.98$, d.f.= 5 and $p < 0.001$.



Note in Figure 4.2 that the slightly shallower slope of the 1992 *vs.* 1993 regression line, was not significantly different from the 1993 *vs.* 1994 slope ($t = 0.361$, d.f.= 10, $p>0.9$). Thus, a single regression line, described by the function $y = 0.79x + 0.12$, was fitted to the entire data set (not shown). To obtain a linear function that accounts more realistically for the changes in canopy conditions, a further regression line was fitted, this time setting the *y* intercept at zero (Fig. 4.3). In other words, the relationship between light conditions in consecutive years is given by

$$\text{light at } t+1 = (0.81) \text{ light at } t \qquad (2)$$

Figure 4.3 Relationship between diffuse light (given as % canopy openness) at times t and t+1 for the entire 1992-1994 data set. The fitted regression line and the coefficients are given in the upper left hand corner. $R^2= 0.98$, d.f.=12, $p<0.001$



Consider a hypothetical gap with 16% canopy openness ($t = t_0$). According to eq. (2) the change in the light conditions through time would occur as follows:

16% x (0.81) = 12.96% at t_1

12.96% x (0.81) = 10.50% at t_2

10.5% x (0.81) = 8.50% at t_3

The way in which light conditions change in time as illustrated by iterating eq. (2) is given by the exponential curve

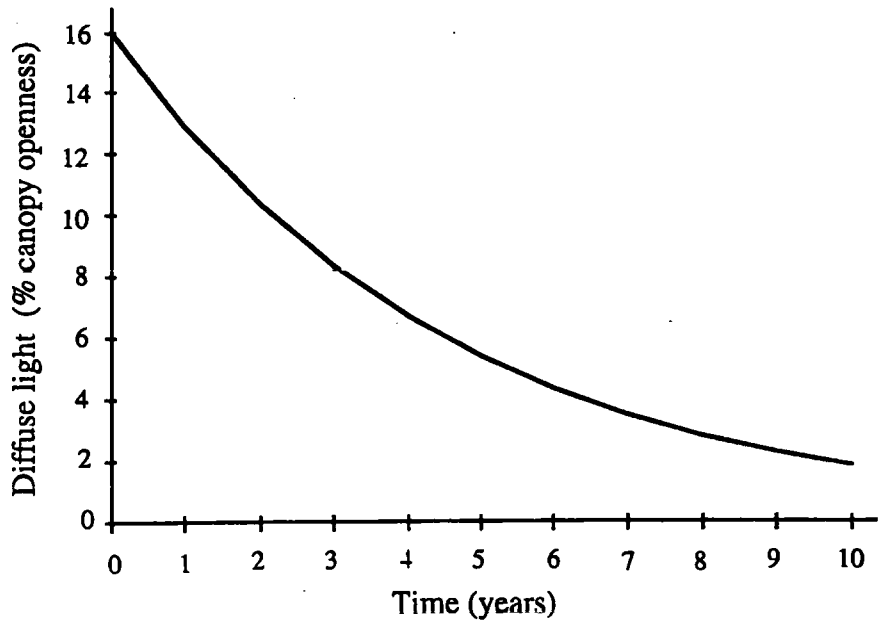
$$y = y_o e^{-ct} \qquad (3a)$$

and

$$t = \frac{\ln \frac{y}{y_o}}{-c} \qquad (3b)$$

where y is diffuse light, y_o is diffuse light at t = 0, and c = ln (0.81) = - 0.21 (Fig. 4.4). The constant, c, represents the exponential rate of change of diffuse light, defined here as the *rate of canopy closure.*

Figure 4.4 Exponential change of diffuse light through time given by $y = y_o e^{-(0.21)t}$



Given the rate of canopy closure, the time required for a certain amount of canopy closure to occur can be calculated from eq. (3b). For example, the time required for a gap with 16% canopy openness to shrink to 7% canopy openness is calculated as:

$$t = \frac{\ln \frac{7}{16}}{-(0.21)} = 3.93 \text{ years}$$

4.3.2 Patch-type Evaluation

In order to characterize forest structure and to describe patch dynamics as a Markov-chain process of forest succession following disturbance (as described in section 4.2.2), four patch types were defined along the light conditions in which *P. vulgaris* populations are usually found in woodland habitats (Table 4.2). The range of light conditions defining each patch type was chosen along a geometric series, according to the exponential canopy closure rate described in the previous section.

Table 4.2 Characterisation of patch types in terms of light environment.

Patch-type	General Description	Diffuse Light (% Canopy Openness)	Centre of category (diffuse light)
1	Big Gap	8 - 16%	12%
2	Small Gap	4 - 8%	6%
3	Closing Canopy	2 - 4%	3%
4	Closed Canopy	1 - 2 %	1.5%

Given the rate of canopy closure, the time required for a certain patch-type to advance to the following patch-type can be approximated as the time required to go from the centre of one patch-type category to the centre of the next category. Thus, the time required for a typical type-1 patch to become a typical type-2 patch is

$$t = \frac{\ln \frac{6}{12}}{-(0.21)} = 3.30 \text{ years}$$

Because patch types were defined along a geometric series and canopy closure was found to be exponential, the time required for any patch-type to become the following patch-type is *constant* (3.3 years), and full canopy closure occurs after 9.9 years. This patch-type classification is therefore referred to as 'uniform'.

A second patch type classification was attempted to investigate how this variable affected the projected forest structure. In chapter 3 it was suggested that the relationship between local population growth rate (λ) and diffuse light is linear (Fig. 3.3). Thus, I can expect that a certain change in light conditions will bring about a change of the same magnitude in λ. Accordingly, I re-defined patch types in terms of the observed relationship between local population dynamics and light conditions along a linear scale (Table 4.3). In this new classification, changing from any patch-type to the following patch-type will be expected to produce an equivalent effect on local population dynamics.

Table 4.3 Alternative characterisation of patch types in terms of light environment along a linear scale.

Patch-type	General Description	Diffuse Light (% Canopy Openness)	Centre of category (diffuse light)
1	Big Gap	12 - 16 %	14%
2	Small Gap	8 - 12 %	10%
3	Closing Canopy	4 - 8 %	6%
4	Closed Canopy	0 - 4 %	2%

According to the patch-type classification proposed in Table 4.3, the time required for each patch-type to advance to the following patch-type was calculated as follows:

for a type-1 patch to become a type-2 patch, $t = \frac{\ln \frac{10}{14}}{-(0.21)} = 1.60$ years

for a type-2 patch to become a type-3 patch, $t = \frac{\ln \frac{6}{10}}{-(0.21)} = 2.43$ years

for a type-3 patch to become a type-4 patch: $t = \frac{\ln \frac{2}{6}}{-(0.21)} = 5.23$ years

Similarly, the time to canopy closure after gap formation (the time required for a type-1 patch to become a type-4 patch) would be an estimate of 9.27 years. This alternative patch-type classification is referred to as 'non-uniform'.

4.3.3 Canopy Dynamics

Matrices in Table 4.4 were built to describe canopy dynamics using the 'uniform' and 'non-uniform' patch-type categories (as defined in Tables 4.2 and 4.3, respectively). Matrix entries, i.e. transition probabilities between patch-types in one year, were calculated from the time required for each patch-type to become the following patch-type. If a type-x patch takes n years to change to the following type-y patch, then, on average $\frac{1}{n}$ of type-x patches will become type-y patches every year, whereas $1 - \frac{1}{n}$ will remain in the type-x category.

Table 4.4 Matrix models of canopy dynamics based on: A) the 'uniform' patch-type classification and B) the 'non-uniform' patch-type classification. All columns sum to unity. k = disturbance regime.

		Patch type at time t			
	A)	**1**	**2**	**3**	**4**
Patch	**1**	0.69	0	0	k
type	**2**	0.31	0.69	0	0
at time	**3**	0	0.31	0.69	0
t+1	**4**	0	0	0.31	1-k

	B)	**1**	**2**	**3**	**4**
Patch	**1**	0.36	0	0	k
type	**2**	0.64	0.58	0	0
at time	**3**	0	0.42	0.80	0
t+1	**4**	0	0	0.20	1-k

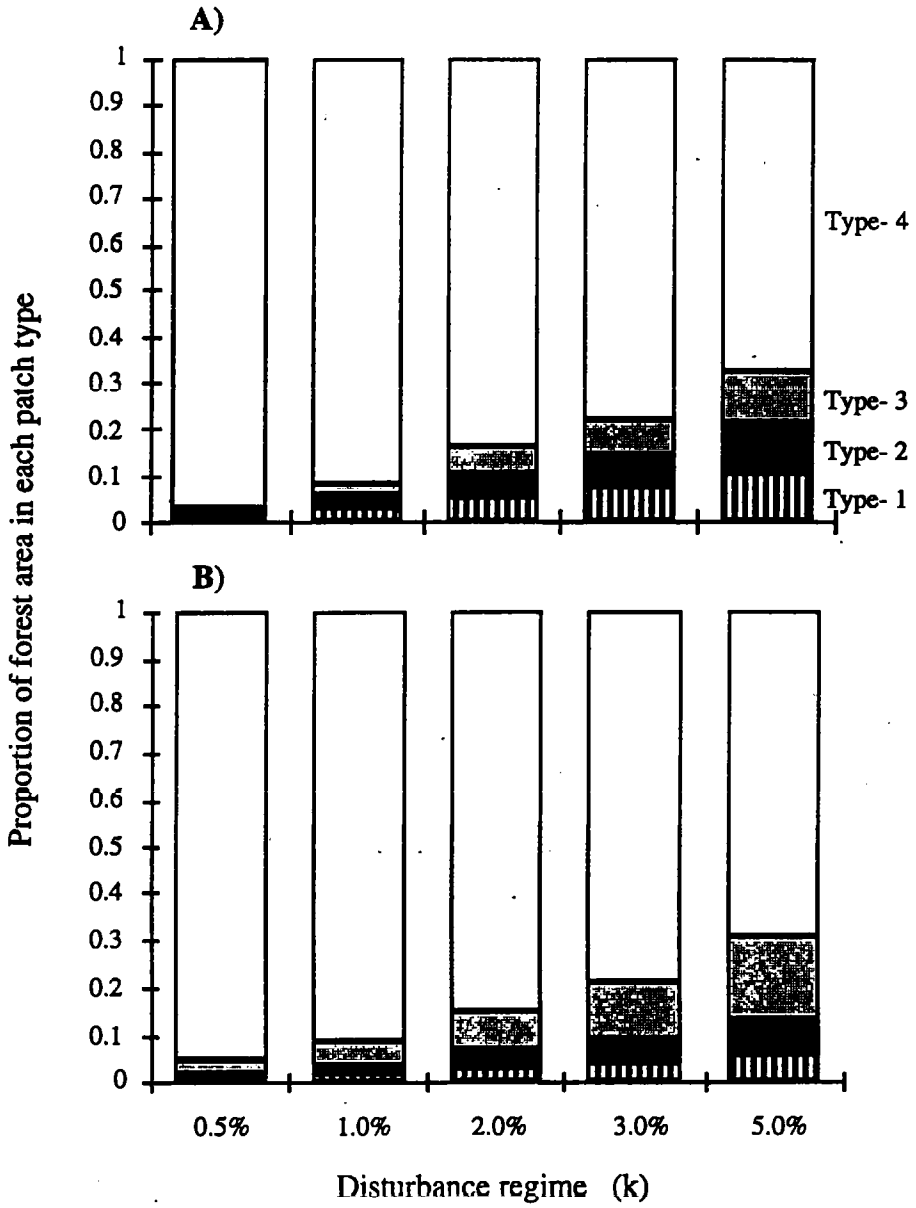
The probability of gap formation in closed canopy patches (matrix entry $p_{1,4}$) corresponds to the disturbance regime, k, i.e. the rate at which canopy gaps are formed. It can be measured as the proportion of the forest area that is affected by natural disturbances each year. Despite the differences in vegetation types and nature of disturbances involved, temperate forests show little variation in this parameter ranging from around 0.5% to 2.0% of forest area per year (Runkle 1985; Runkle and Yetter 1987). Similar k values have been obtained in tropical and sub-alpine forests (Brokaw 1985b; Veblen *et al.* 1994). In this study I considered several k values to test the effect of this variable on forest structure.

Using a Pascal program for matrix iteration written by Elena Alvarez-Buylla, I obtained the dominant right eigen-vectors of matrices in Table 4.4, which are proportional to the 'stable patch-type distributions'. The results are shown in Figure 4.5.

In the case of the 'uniform' patch type distribution, patches 1, 2 and 3 show the same relative frequency at equilibrium (Fig. 4.5A). The 'non-uniform' patch type classification resulted in a different relative frequency of patches 1, 2, 3 and 4; the forest is dominated by type-4 patches, but type-3 patches were more frequent than type-2 patches, which in turn were more frequent than type-1 patches for all k values. This follows from the fact that darker patches require longer time to become the following patch type in the 'non-uniform' patch type classification.

Fig. 4.5 demonstrates that the calculated forest structure at equilibrium was strongly affected by the disturbance regime, but only slightly affected by the patch type classification used. The proportion of the forest area under completely closed canopy varied from 95.4% with a disturbance regime of 0.5%, to 67.4% with a disturbance regime of 5% with the 'uniform' model, and from 95.7% to 69.1% respectively with the 'non-uniform' one.

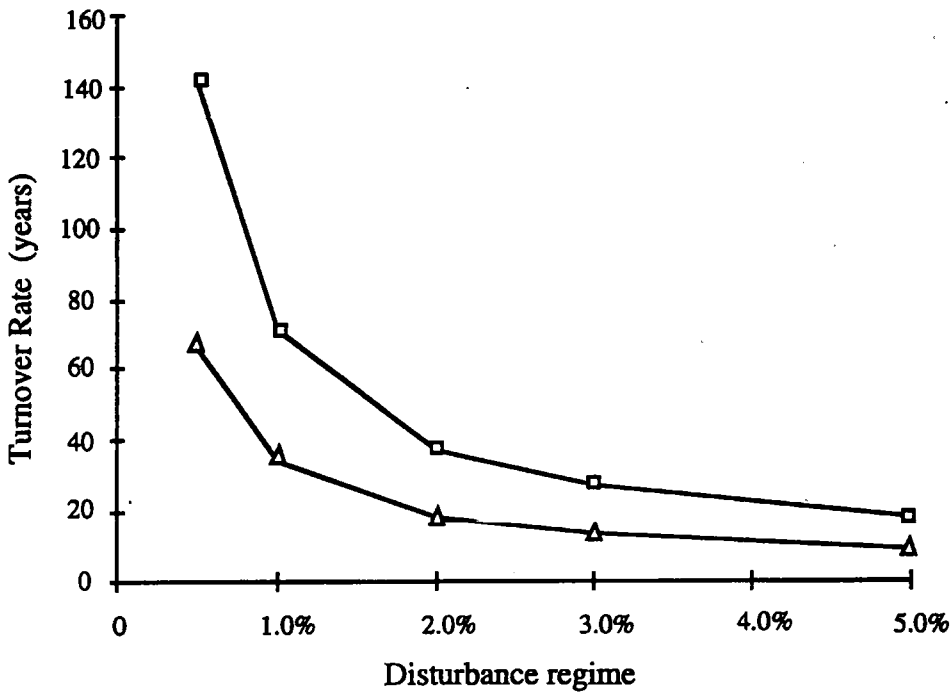
Figure 4.5 Stable patch type distributions for different disturbance regimes (k) resulting from A) 'uniform' patch type classification (Table 4.4A) and B) 'non-uniform' patch type classification (Table 4.4B).



The proportion of the forest area in gap phase (type-1 patches) was larger with higher disturbance regimes (Fig. 4.5). As in the 'non-uniform' patch-type classification type-1 patches become type-2 patches at a faster rate relative to the 'uniform' classification, the former resulted in a lower proportion of the forest area in the gap phase. Thus, as shown in Fig. 4.6, there was a strong effect of patch-type classification on turnover rate, which is the mean time between successive gap formations at any one point in the forest (calculated as

the reciprocal of the proportion of forest in gap conditions - Horvitz and Schemske, 1986). Given the range of disturbance regime values tested, the turnover rate varied from 66.67 to 9.26 years in the 'uniform' patch-type classification, and from 142.85 to 18.51 years in the 'non-uniform' patch-type classification.

Figure 4.6 Effect of disturbance regime on turnover rate (mean time between successive gap formations at any one point in the forest) according to the matrices built with the 'uniform' (triangles) and 'non-uniform' (squares) patch-type classification .



4.4 Discussion

The patch dynamics model presented in this chapter is similar in many respects to previous models. For example, in describing the dynamics of a tropical forest, Horvitz and Schemske (1986) assumed ten hypothetical patch-types. Most patches became the following patch-type after one year, except for those that became type-1 patches due to new tree fall gaps. The probability of gap creation increased with patch age in a logistic way, asymptotically approaching the disturbance regime, k. This model was later applied by Cipollini *et al.* (1993, 1994) to a temperate forest in North America.

The model presented in this chapter did not use an age-based patch-type classification; instead patches were classified according to 'stages' along the canopy regeneration cycle. Stage-classified patch dynamics models have been used by Alvarez-Buylla and García-Barrios (1992) and Alvarez-Buylla (1994), who followed the gap categorisation proposed by Whitmore (1978). Under this classification, both size and age of gap were considered to characterise forest patches. In my model patch 'stages' were selected along a quantitative range of canopy openness, based on both the knowledge of the way in which *P. vulgaris* populations respond to canopy closure, and the rate at which canopy closure occurs.

The rate at which canopy gaps close following disturbance will ultimately depend on gap characteristics (e.g. size and shape). Small gaps usually close through the lateral extension of branches of bordering canopy trees (Runkle 1981; Merrens and Peart 1992). Thus, the time required for a small gap to close will be given by the lateral extension rate of bordering trees, a figure reported as 4 to 14 cm per year (Runkle 1982). A relatively faster radial gap closure rate has been suggested by Cipollini *et al.* (1993, 1994), who used data on radial encroachment by canopy trees to give an estimate of 35 cm per year.

The closure of big gaps depends upon both the growth of individual trees into the canopy (i.e. the time required by new saplings to reach a 10-20 m height), combined with the effect the lateral extension of bordering trees. Considering these variables, Runkle (1982) estimated that large gaps may take between 10 and 40 years to close.

According to the model developed here, the time required for canopy closure after disturbance in the forest at Dancers End is between 9.3 and 9.9 years. How realistic this estimate is will ultimately depend, among other things, on the size and type of disturbance and on the tree species involved in the regeneration phase. Comparable estimates for both tropical and temperate woodlands are 8 to 10 years (Horvitz and Schemske 1986; Cipollini *et al.* 1993, 1994). Thus, the results presented here, based on empirical data on canopy

closure, appear reasonable. Also, the obtained exponential canopy closure rate is in agreement with observations that after a gap opens, structural changes are faster during the first stages of gap closure (Horvitz and Schemske 1986), and that the regeneration of gaps occurs at a faster rate just after gap formation, becoming slower as the size of the gap decreases (Brokaw, 1985b).

In order to test how the estimated time required for canopy closure affected the results, I considered a model with twice the number of patch types, which delays the formation of closed-canopy patches to around 20 years. The results are reported in Table 4.5. There is little difference between the turnover rates obtained with 4 and 8 patch types, especially under low disturbance regimes. The disturbance regime had a more dramatic effect on forest structure and turnover rate than did the number of patch types in the model.

Table 4.5 Turnover rates (in years) obtained for two disturbance regimes using models with a different number of patch types, and therefore, different time to canopy closure.

Disturbance Regime (k)	4 patch types (canopy closure at age 9.9)	8 patch types (canopy closure at age 19.8)
1%	34.5	38.5
2%	18.5	25.0

Turnover rates of natural forests have been reported as typically between 50 and 200 years for disturbance regimes of 1-2% (Runkle 1985). The turnover rates I obtained were considerably lower. This resulted from the stage-based patch type classification used; type-1 patches take longer than one year to become type-2 patches, and thus, the proportion of the forest area in the gap phase at any given time, which is inversely related to turnover rate, is consequently quite high.

In conclusion, this chapter has shown that the rate of canopy closure and gap formation strongly affect forest structure, which in turn influences the ecological processes of gap-

dependent understory species (e.g. *P. vulgaris*) at various levels. At the level of local population demography, canopy closure affects population growth rate; this, in turn, relates to metapopulation processes, including local population extinction. On the other hand, the opening of canopy gaps offer sites for potential colonisation and establishment of new populations; thus, colonisation rate must be a function of the disturbance regime. In this way, the metapopulation dynamics of this species is closely coupled with forest canopy dynamics. This chapter has explored and described canopy dynamics aiming towards a more complete picture of the factors and processes that determine the dynamics of a metapopulation of *P. vulgaris*.

Chapter 5. Effect of Forest Regeneration Cycle and Seed Dispersal on Overall Population Dynamics

5.1 Introduction

Local populations of *Primula vulgaris* exist within a constantly changing forest environment. The forest dynamics not only determines the ephemeral nature of the individual populations, but also confers a dynamic character to the system of local populations at a larger scale, resulting in a temporal variability of spatial patterns of the species' presence and abundance in the forest (Hengeveld 1990). Any detailed analysis of the temporal dynamics of such spatially structured populations requires both demographic data across the range of woodland conditions in which this species occurs (as discussed in Chapter 3) as well as careful, long-term monitoring of the forest mosaic (as discussed in Chapter 4) (Alvarez-Buylla and García-Barrios 1993; Cipollini *et al.* 1993; Maurer 1994). Here, I combine the results of the two previous chapters to develop a model that describes the overall population dynamics of *P. vulgaris* in a forest. In this context, *overall population dynamics* is understood as the way in which the abundance pattern of this species (in terms of the total number of individuals) changes in time in the forest as a whole. The model considers the demographic behaviour and dynamics of individual populations in different patch types, the transitions among forest patch-types through gap formation and canopy closure, and the movement of individuals among different patches through seed dispersal (Horvitz and Schemske 1986; Alvarez-Buylla and García-Barrios 1993; Cipollini *et al.* 1993 and 1994).

5.2 Methods

5.2.1. Patch-specific Demography

In Chapter 4, I categorised the range of forest conditions in which *P. vulgaris* typically occurs into four patch types according to the degree of canopy openness (Table 4.2). Here, I consider the demography of hypothetical *P. vulgaris* populations in each of these patch types to describe overall population dynamics within the changing light environment of the forest .

According to this patch-type categorisation, each patch type was represented by at least one of the woodland populations sampled (Table 5.1). This enabled me to use the population projection matrices reported in Chapter 3 to describe patch-specific population dynamics. In cases where two populations belonged to the same patch type, field data from both populations were pooled to build a single projection matrix (Horvitz and Schemske 1995). A total of eight patch-specific projection matrices, $\mathbf{T}_x$, were built for the two periods studied, i.e. one per patch type per year (Table 5.2)

A second approach was also attempted in order to build patch-specific hypothetical matrices. Instead of using the empirical demographic data directly, as described in the previous paragraph, this method involved the calculation of each individual matrix element based on the observed relationship between individual matrix entries and light. The results of this approach as well as the reasons for choosing the one presented in this chapter are given in Appendix C.1.

Table 5.1 Categorisation of the *P. vulgaris* populations studied in four patch types according to light conditions.

	Patch type	Diffuse light (% canopy openness)	Population growth rate (λ)	Population
1992-93:	1	12.01	1.98	DE2
	2	5.95	1.79	DE5
	2	5.65	0.97	WW
	3	3.09	1.04	SF
	3	2.67	1.06	DE3
	4	2.03	1.27	DE4
	4	1.57	1.13	DE6
1993-94:	1	13.21	0.87	DE7
	1	9.12	1.23	DE2
	2	4.88	1.02	DE5
	2	4.78	0.93	WW
	3	3.52	0.95	SF
	3	2.09	0.93	DE4
	4	1.87	0.88	DE3

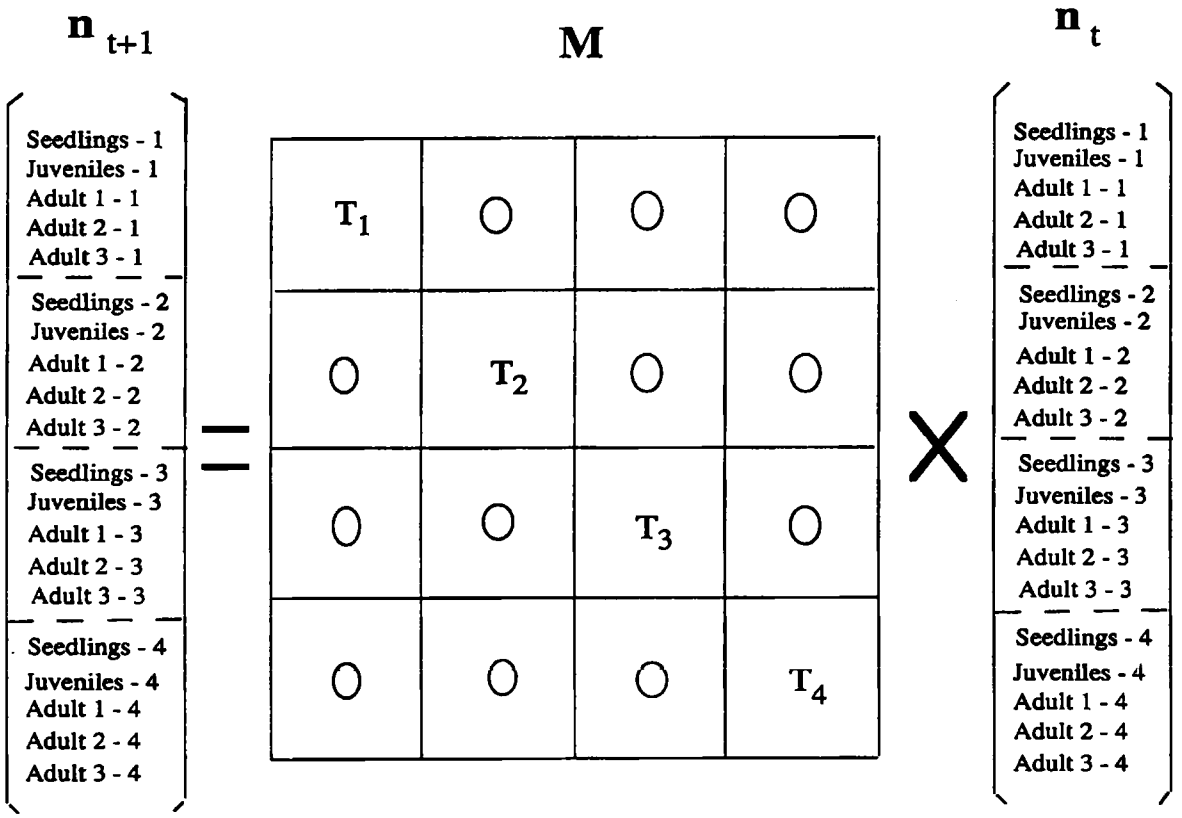
Table 5.2 Source of empirical data used to build patch-specific projection matrices.

	Patch-specific projection matrix	Data source	Population growth rate (λ)
1992-93	T_1	DE2	1.98
	T_2	DE5 & WW	1.44
	T_3	SF & DE3	1.05
	T_4	DE4 & DE6	1.19
1993-94	T_1	DE7 & DE2	1.09
	T_2	DE5 & WW	0.97
	T_3	SF & DE4	0.94
	T_4	DE3	0.88

5.2.2. Overall Population Dynamics

To characterise overall population dynamics, I combined the patch-specific population projection matrices with the Markovian model of canopy dynamics presented in Chapter 4. First, I developed a main matrix model from the patch-specific projection matrices to represent the existence of spatial heterogeneity (Fig. 5.1). Then, I incorporated the canopy regeneration cycle into the model to account for the effect of patch dynamics on overall population growth rate.

Figure 5.1 Main matrix model of overall population dynamics representing spatial heterogeneity.



The overall population of *P. vulgaris* in a forest can be described by a vector, **n**, with a dimension equal to the multiplicative product of the number of plant stage-categories (i.e.,

5) and the number of patch-types (i.e., 4). All possible transitions among stages as well as among patch types can therefore be included in a 20 x 20 matrix, **M**, such that:

$$\mathbf{n}_{t+1} = \mathbf{M}_{abij} \times \mathbf{n}_t \qquad (1)$$

where **M** consists of 16 sub-matrices, $\mathbf{T}_{ij}$; sub-indices *a* and *b* denote rows and columns, respectively, within sub-matrices ($\mathbf{T}_{ij}$); and sub-indices *i* and *j* correspond to rows and columns, respectively, among sub-matrices ($\mathbf{T}_{ij}$). Each matrix entry, $\mathbf{m}_{abij}$, represents the probability that an individual in stage category *b* in habitat *j* contributes to or becomes stage category *a* in habitat *i* in one time step, i.e., one year (Fig. 5.1).

Note in Fig. 5.1 that non-zero sub-matrices are present only along the diagonal; these represent the patch-specific projection matrices, $\mathbf{T}_x$, corresponding type-x populations. All other non-diagonal matrix entries are necessarily set to zero, as this model assumes there are no transitions of individuals among patch types nor changes in patch types in time. In the next two sections, the model is modified to relax these assumptions. An example of matrix **M** for the 1992-93 data set is shown in Appendix C.2.

- Effect of the Forest Regeneration Cycle.

Matrix **M** represents spatial heterogeneity with no migration of individuals among patches or temporal changes among patch types. However, both local populations and forest patches are constantly changing. Using **M** as a basis for modification, a new matrix, **R**, was built that includes the effect of the canopy regeneration cycle, i.e., accounts for the temporal transitions among patch types in the forest. Matrix **R** is similar to **M** but contains non-zero sub-matrices along the leading diagonal, the sub-diagonal and in the upper right hand corner, corresponding to the non-zero probabilities of patches changing categories in time (Fig. 5.2).

The new sub-matrices in **R**, **SubR**, are given by

$$\mathbf{SubR}_{ij} = (p_{ij}) \times (\mathbf{T}_{ij}) \qquad (2)$$

where p_{ij} is the probability of a type-*j* patch becoming a type-*i* patch in one year (see Chapter 4, Fig. 4.1). The sub-matrices in matrix **R** are defined by 1) patch-specific demographies, 2) forest patch dynamics and 3) the timing of gap formation relative to the timing of the annual population census. The latter refers to whether individuals in a type-*j* patch at time *t* will undergo the demographic transitions of type-*j* patches for most of the year, or if instead they will behave according to the demographic transitions expected for a type-*i* patch for most of the year (Horvitz and Schemske 1986). In this study I assumed that tree-falls occur immediately following the census, during late summer or early autumn. Thus, $\mathbf{T}_{ij}$ matrices in equation (2) were actually $\mathbf{T}_{ii}$ (Fig. 5.2).

Figure 5.2 Structure of matrix **R**. $\mathbf{T}_x$ sub-matrices correspond to patch-specific population projection matrices and k is the disturbance regime. The probability of patches changing types over one year was taken from the patch dynamics matrix in Chapter 4 (Table 4.4A).

R

$0.69 \times T_1$	○	○	$(1\text{-}k) \times T_1$
$0.31 \times T_2$	$0.69 \times T_2$	○	○
○	$0.31 \times T_3$	$0.69 \times T_3$	○
○	○	$0.31 \times T_4$	$(k) \times T_4$

The dominant eigen-value of matrix **R** was obtained using MATLAB; this value represents a measure of overall population growth rate (λ_R), i.e. the rate at which total numbers of *P. vulgaris* change in the forest as a whole. The associated column eigen-vector corresponds to the stable category x patch type distribution, i.e. the relative frequency of individuals of different categories in each patch type at the dynamic equilibrium. The effect of different rates of gap formation on overall population dynamics was analyzed by testing different k values in the model (Fig. 5.2). An example of matrix **R** for a disturbance regime, k=1% is given in Appendix 5.3.

- Effect of Seed Dispersal.

Neither matrix **M** nor **R** account for transitions of individuals among patches given by migration. In order to investigate the effect of seed dispersal on overall population dynamics, a further matrix model, **D**, was built. Like **M** and **R**, matrix **D** is composed of *nxn* sub-matrices where *n* is the number of patch types (i.e., 4). Each 5x5 sub-matrix is comprised mostly of zeros; the only non-zero entries are those directly affected by seed dispersal (fecundity elements, d_{13}, d_{14}, and d_{15}). Although migrating diasporas are seeds, the fecundity elements of population projection matrices are based on the number of seedlings emerging per adult in the population. Thus, seed migration was analysed here indirectly, through its effect on seedling emergence (i.e., migration is referred to as 'seedling' dispersal).

To calculate long-distance dispersal I used a slightly different approach to the one used by Horvitz and Schemske (1986) in their study of *Calathea ovandensis*. They estimated the probability of seeds arriving at a particular patch type as a function of only the frequency of that patch type in the environment, and the fraction of seeds dispersing out of populations. Instead, in this study I introduced two new terms to incorporate the effect of the number of 'seedlings' typically produced in the source patch type (r_{bbjj}), as well as the frequency of

both the 'seedling' source (p^*_j) and 'seedling' recipient (p^*_i) patch types in the forest. Considering all these parameters results in a more realistic description of the spatial dynamics of 'seedling' dispersal.

Thus, non-zero elements in matrix **D**, d_{abij}, are given by the number of 'seedlings' arriving in each patch type (immigration) minus the number of 'seedlings' leaving it (emigration):

$$d_{abij} = (r_{bbjj})\,(f_d)\,(p^*_i)\,(p^*_j) - (f_d)\,(r_{abij}) \qquad (3)$$

where r_{abij} are the fecundity elements of matrix **R** presented above, i.e. the number of 'seedlings' produced in each patch type; f_d is the fraction of 'seedlings' dispersing away from the patch, which will be assumed constant for all patch-types; and p^*_j and p^*_i are the relative frequency of type-*j* and type-*i* patches in the forest. The relative frequency of each patch type at equilibrium is given by vector p*, the dominant right eigen-vector of the gap dynamics model represented by matrix **P** (Chapter 4, Table 4.4A). Note that eq. (3) distinguishes r_{bbjj}, i.e. the seed source patch, from r_{abij}, i.e. the seed recipient patch.

In other words, the number of stage class *a* individuals found in a type-*i* patch that come from stage class *b* individuals in a type-*j* patch will be given by the fraction of 'seedlings' reaching a type-*i* patch, i.e., the first term in eq. (3), minus the fraction of 'seedlings' leaving it, i.e., the second term in eq. (3). Appendix C.4 gives an example of matrix **D** for k=1% and f_d=0.2.

- Integrated Effect of Seed Dispersal and Forest Regeneration Cycle.

Note that the dispersal matrix, **D**, is not a self-standing population model; it does not have a direct ecological interpretation. Instead, it was built for the purpose of incorporating seed dispersal among patch types into the model to obtain a further matrix, **E**, given by

$$\mathbf{D} + \mathbf{R} = \mathbf{E} \qquad (4)$$

Thus, matrix **E** describes overall population dynamics, including the effects of both canopy regeneration cycle and seed dispersal. The structure of **E** is similar to **R**; the only differences lie in the fecundity elements in the top row of each sub-matrix, which have been modified by the addition of **D** to account for seed dispersal. The dominant eigen-value of **E**, λ_E, represents the overall population growth rate (i.e. the rate at which total number of *P. vulgaris* individuals change in the forest as a whole) taking into account both canopy dynamics and seed dispersal. To test the effect of disturbance regimes and seed dispersal values on overall population dynamics, the model was run (using MATLAB) with varying k and f_d values. An example of matrix **E** with k=1% and f_d= 0.2 is given in Appendix C.5.

5.3 Results

5.3.1 Patch-specific Demography

Four projection matrices were built to describe patch-specific population dynamics for each period studied (Table 5.3). In those cases where data from two populations were pooled to build a single projection matrix, the combined patch-specific population growth rate (λ) was always intermediate between the λ values of the two populations considered separately.

The direction of demographic changes in relation to light conditions illustrated in Chapter 3 was maintained in these new patch-specific matrices. Mortality of small/young stages generally increased as light availability decreased in the different patch-types. Also, fecundity was higher in populations under brighter conditions. Stable stage distributions were dominated by young/small individuals under relatively open conditions and progressively biased towards adults in darker patches. The second period was characterised by higher mortalities and lower fecundities compare to the first period. All population types

showed positive growth rates in 1992-93 (Table 5.3a). In contrast, only one population showed a positive growth rate in 1993-94 (type-1, see Table 5.3b).

I did not perform any other analyses (e.g. sensitivity, elasticity, or λ confidence intervals) on these patch-specific projection matrices as my aim was not to present a detailed dissection of the demography of these hypothetical populations. Instead, their purpose was simply to provide realistic elements to construct an overall population model that accounts for spatial heterogeneity, canopy dynamics and seed dispersal.

5.3.2 Overall Population Dynamics

- Effect of the Forest Regeneration Cycle.

The results of the overall population model taking into account spatial heterogeneity and canopy dynamics (matrix **R**) are summarised in Fig. 5.3. According to the model, increasing the disturbance regime had a positive effect on overall population growth rate (λ_R) for both periods; under higher disturbance regimes a larger proportion of the forest area is occupied by gaps, where local populations grow at a faster rate relative to closed canopy conditions. Note that the λ_R derived from the overall population dynamics model is different from a simple arithmetic mean of the individual λ values in different patches obtained by weighting the λ of each patch-type by its relative frequency in the habitat. For example, the weighted arithmetic mean for the 1992-93 data set when k=1% is 1.22, whereas the model predicts a λ_R value of 1.41 for the same conditions. The arithmetic mean underestimates the overall population growth rate given by the dynamic model as it does not take into account transitions among patch types in time.

Table 5.3a Patch-specific projection matrices, stable stage distributions and stage-specific mortalities (Qx) for the period 1992-93. Population growth rate (λ) is given on top of each matrix. Plant categories are S=seedlings, J=juveniles, A1= small adults, A2=intermediate adults, A3=large adults (see Chapter 3). Diagonal matrix elements are underlined and fecundity entries are in bold type to facilitate reading.

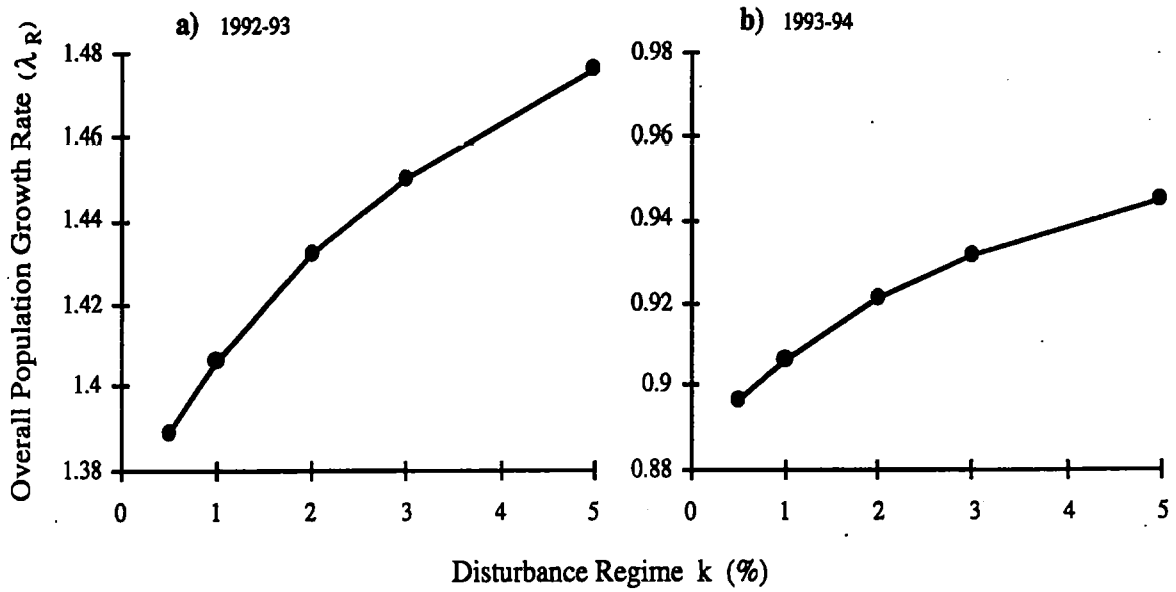
a)	S	J	A1	A2	A3	Stable stage distribution
Type-1		λ=1.976				
S	0	0	**4.469**	**22.900**	**44.900**	0.634
J	0.588	0.423	0.025	0	0	0.241
A1	0.020	0.454	0.562	0.120	0	0.089
A2	0	0.021	0.375	0.780	0.630	0.033
A3	0	0	0	0.100	0.330	0.002
Qx	0.392	0.103	0.038	0	0.037	
Type-2		λ=1.441				
S	0	0	**0.930**	**2.196**	**7.984**	0.469
J	0.440	0.301	0.036	0.004	0	0.188
A1	0.120	0.506	0.504	0.222	0	0.191
A2	0	0.096	0.370	0.631	0.400	0.124
A3	0	0	0.045	0.129	0.580	0.028
Qx	0.440	0.096	0.045	0.013	0.020	
Type-3		λ=1.045				
S	0	0	**0.011**	**0.087**	**0.240**	0.121
J	0.333	0.286	0.024	0	0	0.056
A1	0.1	0.536	0.380	0.049	0.027	0.102
A2	0	0.143	0.503	0.595	0.197	0.310
A3	0	0	0.067	0.347	0.769	0.410
Qx	0.567	0.036	0.025	0.009	0.007	
Type-4		λ=1.191				
S	0	0	**0.210**	**0.383**	**0.825**	0.258
J	0.333	0.333	0.005	0.007	0	0.103
A1	0.286	0.540	0.420	0.128	0.009	0.206
A2	0	0.079	0.378	0.540	0.238	0.213
A3	0	0.016	0.154	0.317	0.733	0.220
Qx	0.381	0.032	0.043	0.007	0.019	

Table 5.3b Patch-specific projection matrices, stable stage distributions and stage-specific mortalities (Qx) for the period 1993-94. Symbols as in Table 5.3a.

b)	S	J	A1	A2	A3	Stable stage distribution
Type-1		λ=1.088				
S	0	0	**0.300**	**3.220**	**6.330**	0.463
J	0.277	0.438	0.087	0.035	0	0.228
A1	0.022	0.262	0.582	0.202	0.100	0.184
A2	0	0.007	0.218	0.647	0.420	0.109
A3	0	0	0	0.087	0.480	0.015
Qx	0.701	0.294	0.114	0.029	0	
Type-2		λ=0.972				
S	0	0	**0.047**	**0.167**	**0.480**	0.115
J	0.325	0.414	0.112	0.0108	0	0.142
A1	0.053	0.329	0.587	0.245	0.041	0.342
A2	0	0.014	0.224	0.615	0.337	0.308
A3	0	0	0	0.112	0.602	0.093
Qx	0.623	0.243	0.076	0.018	0.020	
Type-3		λ=0.945				
S	0	0	**0.013**	**0.094**	**0.176**	0.097
J	0.148	0.207	0.070	0.010	0	0.040
A1	0.016	0.276	0.490	0.104	0.048	0.154
A2	0	0.069	0.210	0.658	0.297	0.420
A3	0	0	0.010	0.208	0.636	0.288
Qx	0.836	0.448	0.220	0.020	0.019	
Type-4		λ=0.879				
S	0	0	**0.019**	**0.185**	**0.521**	0.137
J	0.088	0.400	0.127	0.015	0	0.117
A1	0	0.200	0.549	0.219	0.046	0.308
A2	0	0	0.127	0.657	0.356	0.337
A3	0	0	0.028	0.058	0.598	0.101
Qx	0.912	0.400	0.169	0.051	0	

The λ_R values obtained fell into a relatively restricted range (1.39 - 1.48 in 1992-93 and 0.90 - 0.94 in 1993-94) considering the disturbance regimes tested varied by an order of magnitude (0.5-5%). In fact, the yearly variation in patch-specific demography had a more dramatic effect on λ_R than did the disturbance regime.

Figure 5.3 Overall population growth rate (λ_R) under different disturbance regimes taking into account the forest regeneration cycle for the a) 1992-93, and b) 1993-94 periods. Note the different scale in the *y* axis of a) and b).

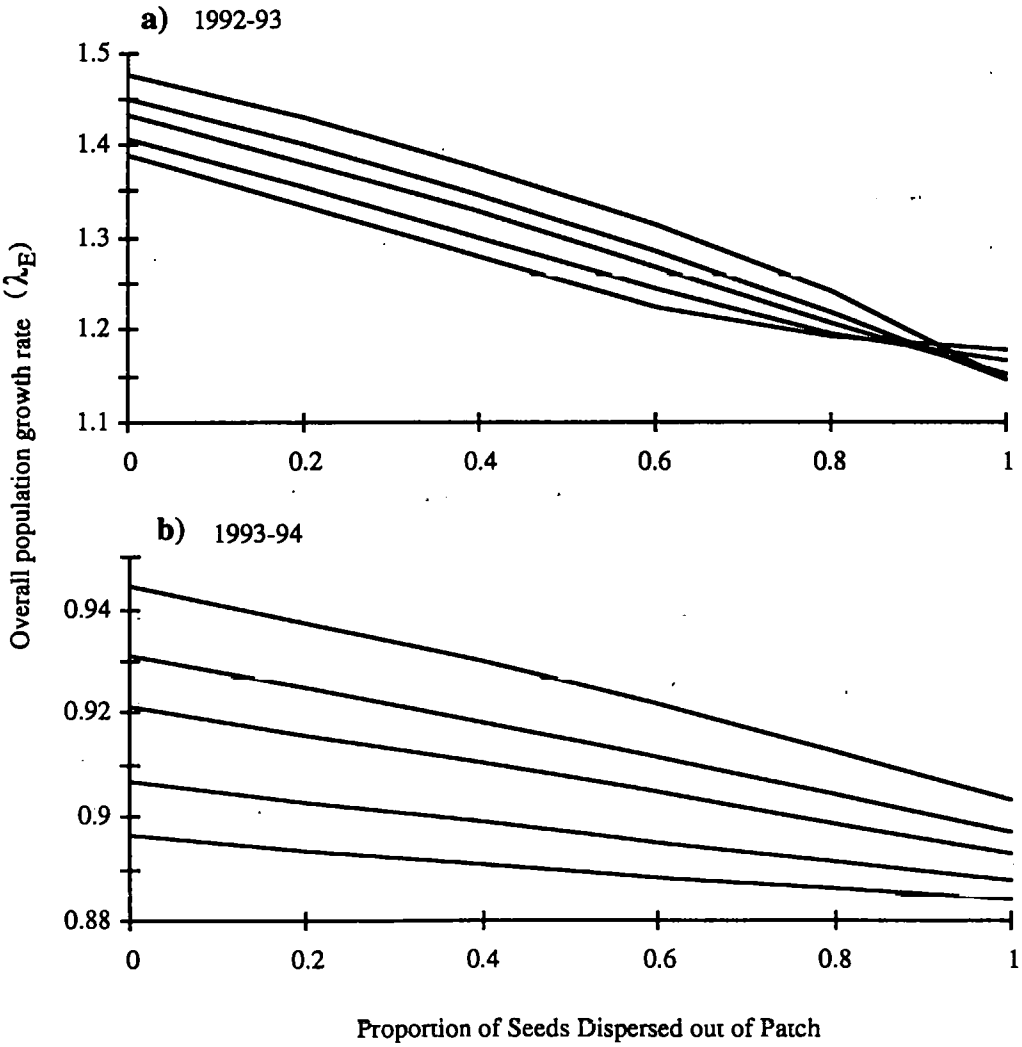


- Integrated Effect of Seed Dispersal and Forest Regeneration Cycle.

Figure 5.4 shows the effect of seed dispersal on overall population growth rate (λ_E) for various disturbance regimes. The range of seed dispersal values tested was 0, 20, 40, 60, 80 and 100% of seeds dispersing out of populations. Higher disturbance regimes were associated with larger λ_E values. However, λ_E decreased with increasing proportion of seeds dispersed out of the patches. Generally, the sensitivity of overall population growth rate to changes in the proportion of seeds dispersed out of patches was greater under higher disturbance regimes (shown in Fig. 5.4 by the greater slopes of the lines representing higher disturbance regimes).

Overall population growth was always positive in 1992-93 and negative in 1993-94 for all combinations of seed dispersal and disturbance regimes tested. The range of variation in λ_E was smaller for the second period (0.884 - 0.945) than for the first period (1.145 -1.476). Again, the variation in overall population growth rate between the two periods studied was larger than the effect of either the disturbance regime or seed dispersal.

Figure 5.4 Effect of seed dispersal on overall population growth rate (λ_E) for the periods a) 1992-93 and b) 1993-94. The different lines in each graph correspond to disturbance regime values of 5, 3, 2, 1 and 0.5% (from top to bottom). Note the different scale in the y axis of a) and b).



5.4 Discussion

Empirical data on *P. vulgaris* population dynamics and canopy closure have allowed me to describe in some detail the system formed by this species and the habitat it occupies. This chapter focuses on two elements of this system: the way in which demography changes along forest patches in different stages of the forest regeneration cycle, and the rate at which canopy closure occurs. However, a variety of other factors must affect the system's behaviour in many different ways; in particular, seed dispersal and gap opening rate (disturbance regime) might play a crucial role. Although no empirical data on seed dispersal or disturbance regime were available for the specific sites I worked on, it was possible to illustrate the effect of such variables on overall population dynamics by plugging different hypothetical values into the model. I chose hypothetical disturbance regime values of 0.5 to 5%; this range includes the 1-2% k values reported for other temperate woodlands (Runkle 1985; Runkle and Yetter 1987).

According to patch-specific demographic behaviour, population growth rate is higher in type-1 patches. By definition, higher disturbance regimes result in a larger proportion of the forest under type-1 conditions; hence, overall *P. vulgaris* numbers in the forest would be expected to increase with increasing disturbance regime, which is exactly what the model predicts. Similar results have been reported using an equivalent model with a gap-dependent tropical understory herb, *Calathea ovandensis* (Horvitz and Schemske 1986) and a temperate understory shrub, *Lindera benzoin* (Cipollini *et al.* 1994). These results have important implications for forest management, as the opening of new gaps in a forest occurs through both natural disturbances and coppicing. The gradual loss of traditional coppicing practices in a great number of ancient woodlands in Britain could lead to a decrease in the abundance of understory species such as *P. vulgaris* (Barkham 1992a).

With regards to seed dispersal, the model predicts that higher proportions of seeds being dispersed out of populations will result in lower overall population growth rates. One of the consequences of seed dispersal is that it results in an increased presence of seedlings in closed canopy patches (since they are the most frequent kind in the environment), where population growth rate is lowest. Also, adding net seed dispersal (calculated from eq. 3, given by entries in matrix **D**) to matrix **R** reduced all non-zero fecundity elements (compare Appendices C.3 and C.5). In this context, seed dispersal implies 'seedling' loss because the number of 'seedlings' leaving a patch is always higher than the number arriving as part of the seed rain. This reflects the high risk involved in seed dispersal; the amount of emigration can significantly exceed that of immigration, especially in spatially structured populations where occupied patches are embedded in a system primarily composed of patches unsuitable for germination and establishment (Horvitz and Schemske 1986; Cipollini *et al.* 1993, 1994).

Long-distance seed dispersal (i.e. occurring beyond the boundaries of a population) represents a cost from the points of view of both the individual and the population. On the one hand, there is a high energy allocation cost of producing dispersal structures (e.g., elaiosomes, wings, pulp); on the other hand, dispersed seeds have to face high mortality risks due to the decreased probabilities of landing in safe sites for germination or as a result of 'handling' by dispersal vectors. As a consequence, long-distance seed dispersal may represent a reduction in individual fitness as well as population growth rate (Murray 1986; Venable and Brown 1993).

In the case of *P. vulgaris*, seed dispersal certainly represents a risky phase. Seeds may be transported by ants and rodents (Keith-Lucas 1968; Richards 1989). Obviously, seed dispersed by ants would be more likely to escape the risk of rodent predation (Turnbull and Culver 1983; Bond and Breytenbach 1985; Kjellson 1985; Hughes and Westoby 1990). However, at Dancers End it appears that ants harvest only a small proportion of the seeds

available, even in patches where ants are abundant (next to grassland areas). At this site, rodents were primarily responsible for the observed high seed removal rates (50-60% - Valverde and Silvertown, in press, Appendix A). Seed removal must play a major role in decreasing seedling recruitment in these populations and the results presented here illustrate how this might affect overall population dynamics. Whether those seeds actually survive and reach other forest patches remain to be investigated. Some rodents from temperate habitats may store between one third and one fifth of their harvest, acting both as seed dispersers and seed consumers (Price and Jenkins 1986). In the case of *P. vulgaris*, seeds harvested by rodents would face not only the risk of landing in unsuitable patches, but also the high probability of being eaten by their potential dispersal vector. Nevertheless, this potential long-distance dispersal might play an important role in allowing the arrival of seeds at newly-opened gaps.

Venable and Brown (1993) developed a model about the population dynamics consequences of dispersal and concluded that long-distance dispersal decreases the arithmetic mean fitness of populations. The results for *P. vulgaris* presented in this chapter also illustrate the population dynamics costs of long-distance seed dispersal: seeds leaving the population have high probabilities of landing in unfavourable closed canopy patches and this can reduce overall population growth rate. In their study of *Calathea ovandensis*, Horvitz and Schemske (1986) reached similar conclusions and therefore, suggested that selection should act *against* long-distance dispersal. However, note that these models did not consider any density-dependent effects. A different scenario would result if there was, in fact, a reduction of density-dependent seedling mortality as a result of long-distance seed dispersal (Murray 1986), which could counteract the effect of the high seed mortality resulting from landing in unfavourable patches.

Also, the time-scale used to evaluate the effects of long-distance seed dispersal on plant fitness must be considered. For plants that occupy rather ephemeral sites, such as canopy gaps, long-distance seed dispersal is important to long-term individual fitness (Silvertown

1991), as it allows the arrival of seeds at potentially colonisable patches. Turning towards the metapopulation perspective, this process is what ultimately allows the foundation of new local populations. The following chapter presents some results relevant to this issue.

Chapter 6. Metapopulation Dynamics

6.1 Introduction

Some populations do not function as spatially-isolated units, but instead form groups or arrays of populations which give rise to a *metapopulation*, i.e., a system of local populations connected by dispersing individuals (Levins 1970). Hanski and Gilpin (1991) have defined it as an abstraction of the population concept at a higher level in which a different spatial and temporal scale are considered. At a local scale, 'populations' refer to groups of interacting individuals of the same species. At a larger scale, 'metapopulations' arise as dynamic systems of such local populations (Hanski 1989; Hanski and Gilpin 1991). Analogous to birth and death processes at the population scale, colonisation and extinction of local populations describe the dynamics of the metapopulation. Thus, analysis of metapopulation dynamics involves, among other things, the study of colonisation and extinction rates and the conditions under which these two processes are in balance (Hanski 1991; Hanski and Gilpin 1991).

In Chapter 5 I presented a matrix model that described overall population dynamics of *P. vulgaris* in a forest (in terms of the *number of individuals*), including the effects of both the canopy regeneration cycle and seed dispersal. Here I also examine the effect of these two factors, but this time at the metapopulation level (i.e., in terms of the *number of populations*), thus, incorporating metapopulation processes such as colonisation and extinction.

Many plant species show a spatially discontinuous distribution in which occupied patches are scattered in the habitat. Frequently, this distribution pattern is related to the patchy nature of most natural environments (Picket and White 1985). Whether individual patches should be regarded as separate populations or as local populations functioning as a metapopulation depends upon the degree of interconnection among them (Silvertown and Lovett Doust 1993). In a metapopulation there is a significant flow of individuals linking local populations together and allowing the arrival of individuals at new colonisable patches (Levins 1970).

In the preceding chapters I have suggested that *P. vulgaris* populations are structured in metapopulations. Within a particular forest this species shows a patchy distribution which is largely controlled by the patchiness of the environment resulting from variation in the degree of canopy cover. Each occupied patch has been regarded as a local population. Thus, forest canopy dynamics strongly affect *P. vulgaris* metapopulation processes: the opening of gaps in the canopy allows the establishment of new populations whereas canopy closure may cause population decline and eventual extinction. This results in a permanently changing system in which colonisations and extinctions are constantly taking place.

In this chapter, I develop a model that describes these larger scale metapopulation processes (i.e., colonisation and extinction rates and the role of seed dispersal in connecting local populations) based on the knowledge of some of the elements that most strongly affect them, namely the demography of local populations in different forest patches (discussed in Chapter 3) and canopy dynamics (discussed in Chapter 4). The model presented here accounts for the changes in the number of populations in the metapopulation, given by colonisations and extinctions. The effect of seed dispersal and forest disturbance regime on metapopulation dynamics will then be investigated by introducing these variables into the model.

6.2 Methods

6.2.1 The Metapopulation 'Life-cycle' Graph

A demographic characterisation of a population can be obtained by classifying individuals into categories (e.g. stages, sizes or ages) and by investigating their distribution among these categories. Information on the contributions and transitions of individuals from one category to another in time provides a more detailed picture of population dynamics (Caswell 1989). All these demographic variables can be illustrated in a life-cycle graph such as the one proposed for *P. vulgaris* in Chapter 3 (Fig. 3.2).

A similar approach can be used to characterise a metapopulation. Local populations can be classified into categories according to particular demographic or environmental features. Metapopulation dynamics can be described by the contributions or transitions among the different population categories in time, including new local populations entering the metapopulation (colonisation) and old populations disappearing (extinction). This is equivalent to a traditional demographic analysis, but instead of looking at the demographic fate of individuals within a population, the relevant units are now local populations within a metapopulation.

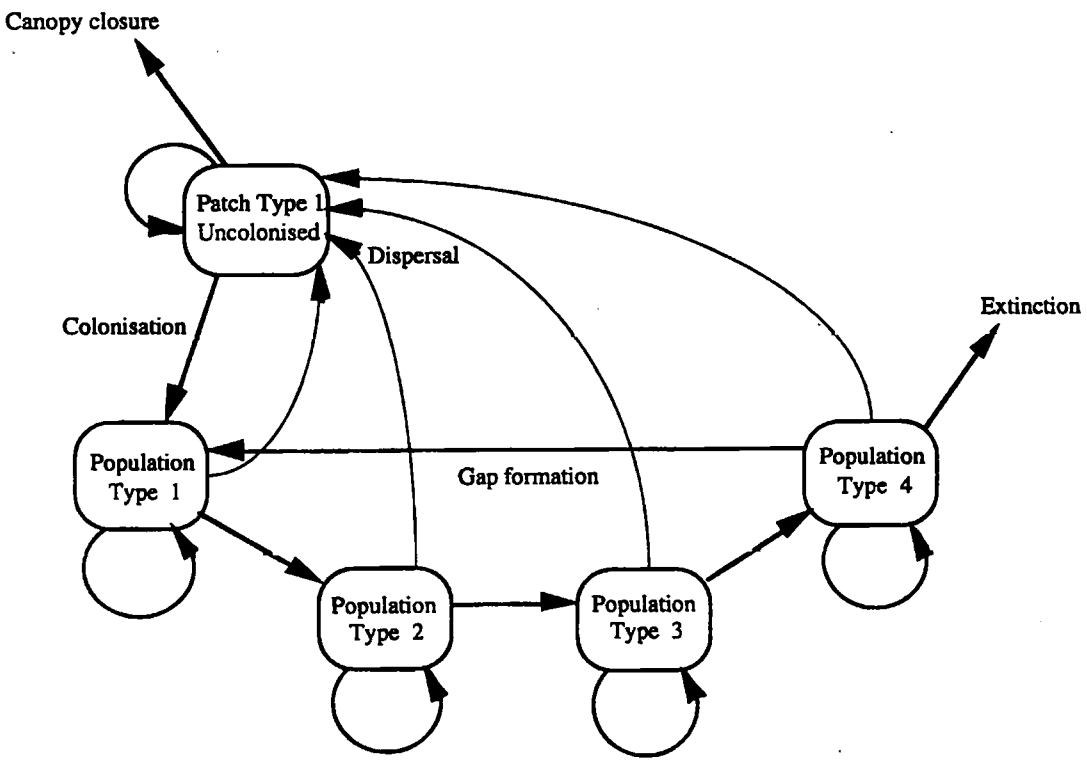
In previous chapters I have categorised the range of forest patches in which *P. vulgaris* typically occurs into four types, defined in terms of diffuse light (Chapter 4). In each patch type, *P. vulgaris* population dynamics has been characterised using patch-specific projection matrices (Chapter 5). In this chapter I consider these four population types to be different stages through which local populations move in time as the forest canopy changes (Table 6.1 - compiled from data in previous chapters).

Table 6.1 Population types and corresponding forest patches (compiled from data presented in Tables 4.2 and 5.2 - patch-specific projection matrices for each population type presented in Table 5.3).

Population Type	Diffuse light (% canopy openness)	Forest Patch	Population growth rate (1992-93 / 1993-94)
1	8 - 16	Big gap	1.98 / 1.09
2	4 - 8	Small gap	1.44 / 0.97
3	2 - 4	Closing canopy	1.04 / 0.94
4	1 - 2	Closed canopy	1.19 / 0.88

The metapopulation 'life-cycle' graph summarises the pathways that local populations may follow as a result of the changes in the forest canopy (Fig. 6.1). The boxes in Fig. 6.1 correspond to the stages through which populations move and the arrows represent the possible fates that each population type might experience over one year.

Figure 6.1 *P. vulgaris* metapopulation 'life-cycle' graph. The boxes are the different stages through which populations/patches move and the arrows represent the possible contributions or transitions among stages within one year.

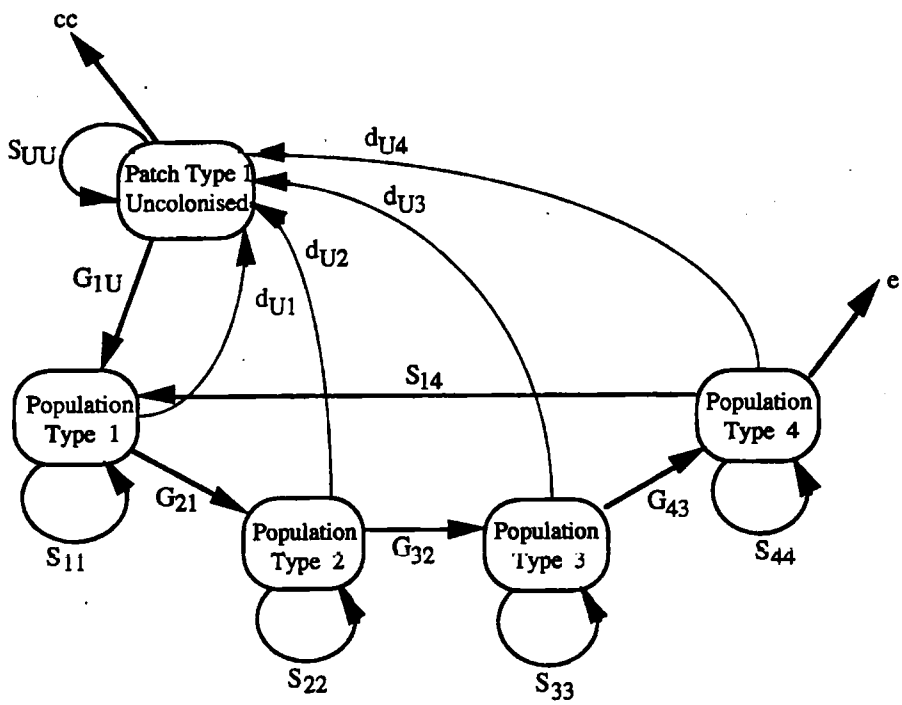


Populations may remain the same or move to the following type; type-4 populations may go extinct or, if a gap opens in the canopy, become type-1 populations. The arrival of seeds at newly-opened gaps (i.e., uncolonised type-1 patches) can occur through seed dispersal from any population type. If enough seeds arrive and become established, uncolonised type-1 patches may become type-1 populations. Alternatively, if a gap is not colonised and the canopy closes, the patch will eventually become unsuitable for colonisation.

The probability of each of these potential fates occurring from one year to the next can be calculated and incorporated into a projection matrix. The correspondence between the metapopulation 'life-cycle' graph and the metapopulation projection matrix is illustrated in Fig. 6.2.

Making an analogy with the structure of a stage-based population projection matrix, seed dispersal to uncolonised type-1 patches (d) would occupy the place of fecundity elements (i.e., contribution of older categories to the first category), whereas the entry in the upper left-hand corner (S_{uu}) would be the equivalent of a seed bank (i.e., 'dormant populations' remaining as potential members of the metapopulation). The remaining matrix elements would correspond to survival (S) and growth (G) probabilities.

Figure 6.2 Correspondence between the metapopulation 'life-cycle' graph and the metapopulation projection matrix. Population types 1-4 are defined in Table 6.1. Matrix elements, m_{ij}, correspond to the probability of a type-*j* population contributing to or becoming a type-*i* population in one years time. Also, uncolonised type-1 patches (U) may become unsuitable for colonisation due to canopy closure (cc) and type-4 patches may go extinct (e).



Metapopulation Projection Matrix

Stage at time t+1 \ Stage at time t	U	1	2	3	4
U	S_{UU}	d_{U1}	d_{U2}	d_{U3}	d_{U4}
1	G_{1U}	S_{11}	0	0	S_{14}
2	0	G_{21}	S_{22}	0	0
3	0	0	G_{32}	S_{33}	0
4	0	0	0	G_{43}	S_{44}

6.2.2 Metapopulation Parameter Estimation

- Transitions Among Population Types

The probability of any *P. vulgaris* population remaining in the same category or moving to the following category in a one year period is given by the probability of forest patches changing types in that same period, which is in turn determined by canopy closure. Using the patch-type classification given in Table 6.1, the time required for each patch type to move to the following category is 3.3 years (Chapter 4, section 4.3.2). Thus, given that a type-*x* population takes *n* years to become a type-*y* population, an average of 1/*n* type-*x* populations will become type-*y* populations every year. Therefore, the probability of any population type becoming the next type after one year (p) is 0.31 (i.e., 1/3.3), whereas the probability of populations remaining in the same category is 0.69 (i.e., 1-p). Note in Fig. 6.2 that the entries G_{21}, G_{32}, and G_{43} each correspond to probability p, whereas S_{11}, S_{22}, and S_{33} are each given by 1-p.

The probability of a type-4 population becoming a type-1 population (S_{14} in Fig. 6.2) is equivalent to the probability of a gap opening in any closed canopy patch in the forest, which is given by the disturbance regime, k. Thus, the probability of a type-4 population remaining as such from one year to the next (S_{44} in Fig. 6.2) is determined by 1-k, less the probability of the population going extinct, as discussed below.

- Extinction Rate

I estimated the extinction probability of a population under completely closed canopy conditions by calculating its expected time to extinction as follows:

The instrinsic rate of natural increase (r) is defined as $r = \ln \lambda$ (1)

where λ is the population growth rate.

Population size (n) at time t+x can be calculated as $n_{t+x} = n_t \, e^{rx}$ (2)

Let x be the expected time to extinction (t_e). Thus, combining eqs. (1) and (2),

$$t_e = x = \frac{\ln \frac{n_{t+x}}{n_t}}{\ln \lambda} \qquad (3)$$

I regard a population as virtually extinct when its number of individuals drops to 5% of initial population size. That is:

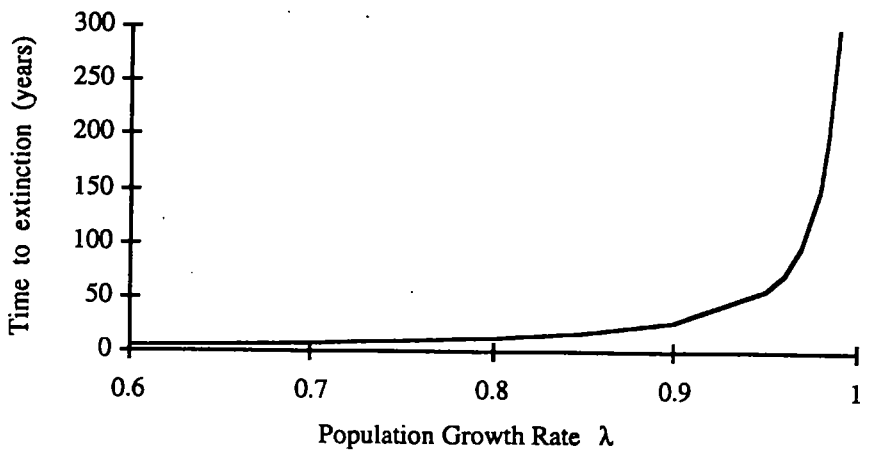
$$\frac{n_{t+x}}{n_t} = 0.05 \qquad (4)$$

Using the lowest λ value obtained for a population under completely closed canopy conditions, λ=0.88 (Table 6.1), the time to extinction is given by

$$t_e = \frac{\ln (0.05)}{\ln (0.88)} = 23 \text{ years}$$

Note that as λ approaches unity, the time to extinction (t_e) increases asymptotically (Fig. 6.3).

Figure 6.3 Time to local population extinction as a function of population growth rate (λ).



In the previous section I calculated the probability of a population changing categories in one year's time by considering the time required for such a transition to occur. Similarly, given that a type-4 population takes 23 years to go extinct, the extinction probability (e_p) of any type-4 population from one year to the next is 0.043 (i.e., 1/23)

-Seed Dispersal

The contribution of established local populations to the colonisation of newly opened gaps occurs through seed dispersal. The probability of 'seedlings' of each population type arriving in a newly-opened gap depends on both the fraction of 'seedlings' dispersing out of the population (f_d, assumed constant for all population types) and the frequency of newly-opened gaps in the environment (disturbance regime, k). Thus, the seed dispersal elements in the matrix illustrated in Fig. 6.2 are given by:

$$d_x = (F_x)\,(f_d)\,(k) \qquad (5)$$

where F_x, the mean fecundity in a type-x population, was calculated as

$$F_x = \frac{\text{No. of seedlings at t+1}}{\text{No. of reproductive individuals at t}} \qquad (6)$$

The mean fecundity in each population type was derived from empirical data obtained from the sampled populations (Table 6.2); the data of populations in similar light environments was pooled in the same way as described in Chapter 5 (Table 5.2). These values, for the 1992-93 and 1993-94 periods, are given in Table 6.2.

Table 6.2 Source of the empirical data used to calculate fecundity for each population type. The demography of these populations (Dancers End: DE, Woburn Wood: WW, and Salcey Forest: SF) was described in Chapter 3. Field data from pairs of populations were pooled before calculating mean fecundity.

	Population Type	Source of data	Mean Fecundity
1992-93	1	DE2	17.29
	2	DE5 & WW	2.73
	3	SF & DE3	0.11
	4	DE4 & DE6	0.41
1993-94	1	DE7 & DE2	2.34
	2	DE5 & WW	0.17
	3	SF & DE4	0.11
	4	DE3	0.24

- Colonisation

Arrival of seeds at a newly opened gap does not necessarily result in the foundation of a new population; the probability of colonisation increases with increasing seed input. Thus, I defined the colonisation parameter (c) as the sum of seed dispersal from all population types:

$$c = \sum d_x \qquad (7)$$

The probability of a gap being colonised depends on both c and the probability of gaps remaining open from one year to the next (as calculated in Chapter 4, section 4.3.2). Therefore, the probability of an unoccupied type-1 patch becoming a type-1 population in one year (G_{1u} in Fig. 6.2) is given by the colonisation parameter multipiled by the probability of a type-1 patch remaining as such (i.e., c x 0.69). The probability of an unoccupied type-1 patch remaining unoccupied (G_{uu} in Fig. 6.2) is (1 - c) x 0.69.

6.2.3 Metapopulation Growth Rate and Elasticity Analysis

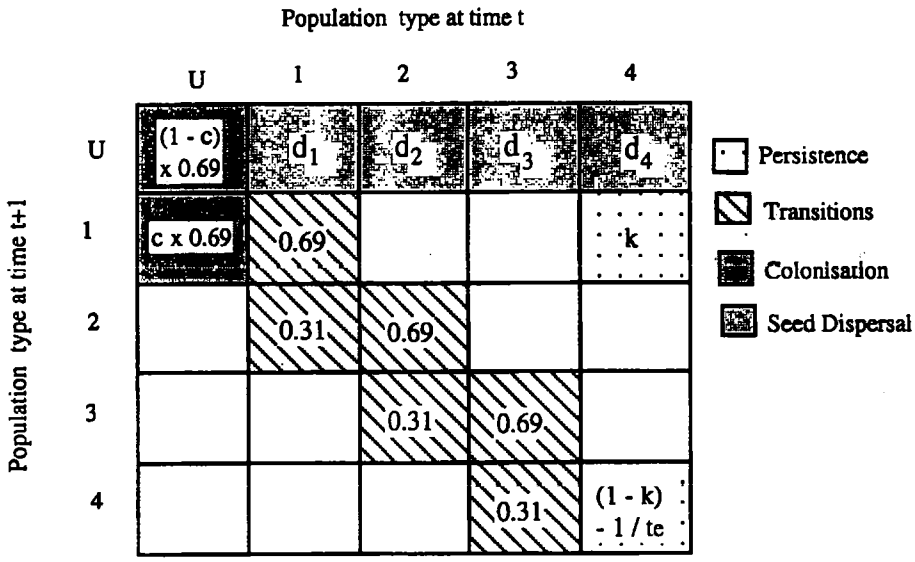
The basic structure of the metapopulation projection matrix defined in terms of the above parameters is illustrated in Table 6.3. Metapopulation growth rate (i.e., the rate at which the metapopulation is increasing or decreasing in number of populations) was obtained as the dominant right eigen-vector of the metapopulation matrix with the aid of a matrix analysis computer program written by E.R. Alvarez-Buylla. Different values of seed dispersal and forest disturbance regime were considered in order to test their effect on metapopulation growth rate. Elasticity matrices were obtained for the various metapopulation projection matrices built. By grouping elasticity values corresponding to specific elements of the 'life-cycle' graph (Fig. 6.2) it is possible to evaluate the relative importance of each of these elements in determining λ (Silvertown *et al.* 1993; van Groenendael *et al.* 1994). Thus, I grouped different elements of the metapopulation elasticity matrices in order to evaluate the relative contribution of the persistence of old populations (P), transitions among population

types (T), colonisation (C), and seed dispersal (D) to metapopulation growth rate. I calculated total elasticity of P, T, C and D by adding the individual entries of the elasticity matrix involved in each case, as described in Fig. 6.4.

Table 6.3 Structure of the metapopulation projection matrix. It is equivalent to the one illustrated in Fig. 6.2 after having defined each matrix entry (c, colonisation parameter; d_x, seed dispersal from a type-x population; t_e, time to population extinction; k, disturbance regime).

	Uncolonised Type-1 patch	Type-1 population	Type-2 population	Type-3 population	Type-4 population
Uncolonised type-1 patch	(1-c) x 0.69	d_1	d_2	d_3	d_4
Type-1 population	c x 0.69	0.69	0	0	k
Type-2 population	0	0.31	0.69	0	0
Type-3 population	0	0	0.31	0.69	0
Type-4 population	0	0	0	0.31	$(1-k) - (1/t_e)$

Figure 6.4 Categorisation of different matrix elements related to seed dispersal, colonisation, transitions among population types, and persistence of old populations.



6.3 Results

Projection matrices were built using various proportions of seeds dispersed out of populations (f_d = 0.01, 0.1, 0.2, 0.4, 0.6, 0.8 and 1.0) and disturbance regime values (k = 0.5, 1, 2, 3 and 5%) for the periods 1992-93 and 1993-94 in order to test their effect on metapopulation growth rate (λ_M). Table 6.4 shows one of these metapopulation projection matrices.

Table 6.4 An example of a metapopulation projection matrix for the 1992-93 period, with disturbance regime k=1%, fraction of seeds dispersing out of populations f_d=0.2, and time to population extinction t_e= 23 years (corresponding to λ = 0.88 for type-4 populations).

	Uncolonised	Type-1	Type-2	Type-3	Type-4
Uncolonised	0.671	0.035	0.005	0.0002	0.0008
Type-1	0.028	0.690	0	0	0.010
Type-2	0	0.310	0.690	0	0
Type-3	0	0	0.310	0.690	0
Type-4	0	0	0	0.310	0.947

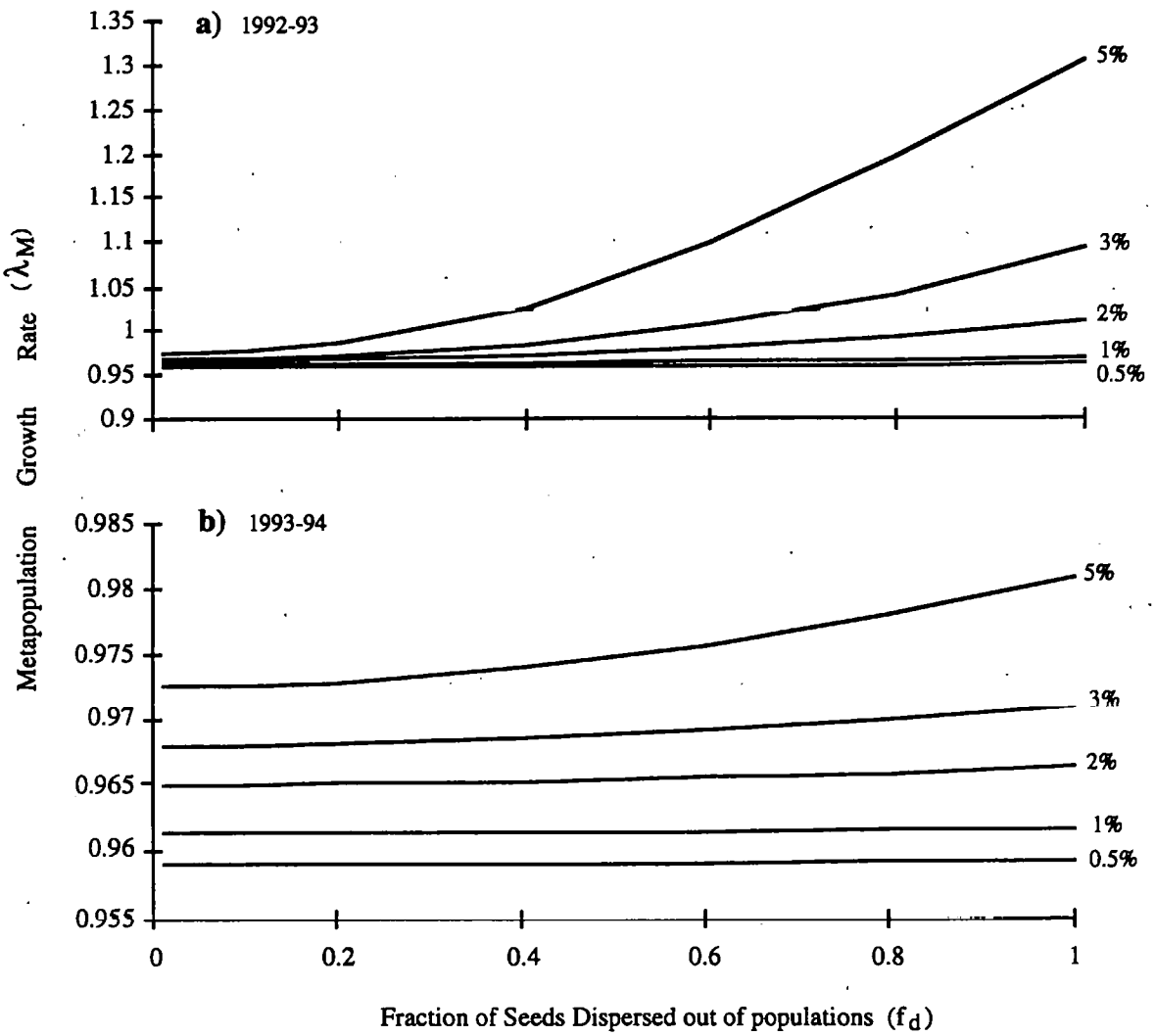
6.3.1 Effect of Seed Dispersal and Disturbance Regime on Metapopulation Growth Rate

Increasing disturbance regime increased metapopulation growth rate because higher disturbance regimes result in a greater proportion of forest patches in gap (and thus, potentially colonisable) conditions (Fig. 6.5). However, with low seed dispersal the difference between λ_M values obtained with various disturbance regimes was moderate, and became more dramatic as seed dispersal increased, particularly for the 1992-93 period.

Seed dispersal had a stronger effect when combined with high disturbance regimes; the range of dispersal values tested produced a variation in λ_M from 0.959 to 0.961 when k = 0.5%, and from 0.973 to 1.305 when k = 5% in 1992-93 (Fig. 6.5a). Seed dispersal

and disturbance regime had a synergistic effect on metapopulation growth rate: disturbance regime had a bigger effect on λ_M at high dispersal levels than at low dispersal levels. This was because higher disturbance regimes produced a higher frequency of colonisable patches in the forest, and high dispersal values increased the probability of those patches being colonised. These trends were apparent in both periods, but more dramatic with the 1992-93 fecundity values. With the 1993-94 data set, λ_M varied only from 0.959 to 0.981 along the entire range of conditions tested.

Figure 6.5 Metapopulation growth rate (λ_M) as a function of seed dispersal and disturbance regime for the periods a) 1992-93 and b) 1993-94. Disturbance regime values are given on the right. Note the different *y* axis scales between both graphs.



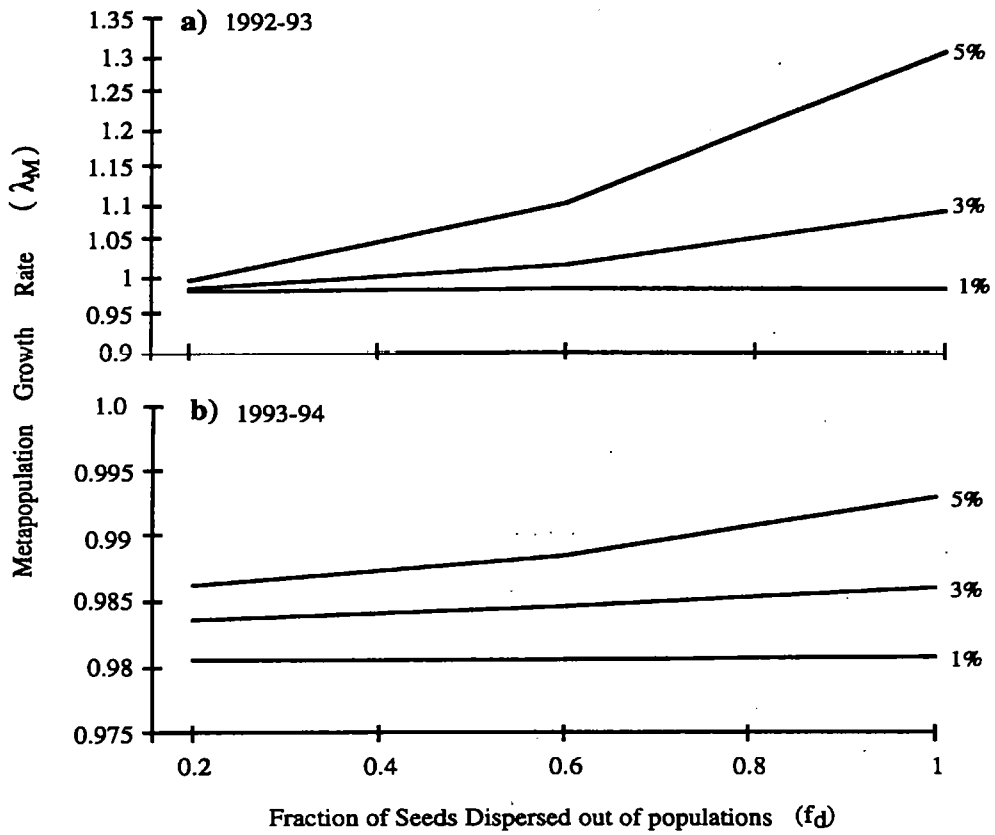
The most significant difference between the two periods was that no 1993-94 λ_M values exceeded unity. This result emphasises that a sufficiently large number of seeds must be produced in existing local populations to generate positive metapopulation growth rates. When fecundities were low, the number of seeds arriving to uncolonised type-1 patches was insufficient to ensure high colonisation rates, even when the seed dispersal was at its highest. On the other hand, the high fecundities recorded in frequently 1992-93 produced positive metapopulation growth rates (e.g., $f_d = 1$ with $k = 2\%$, $f_d = 0.6$ with $k=3\%$, $f_d = 0.4$ with $k = 5\%$).

6.3.2 Effect of Local Population Extinction Rate

The results presented in Fig. 6.5 were based on a time to extinction of 23 years, based on the assumption of $\lambda=0.88$ in type-4 populations. To test the effect of extinction rate on metapopulation growth rate, new metapopulation matrices were built by doubling the time to extinction ($t_e = 46$ years); this corresponds to $\lambda=0.94$ for type-4 populations (Fig. 6.3).

Metapopulation growth rate was obtained as the dominant eigen-value of these new matrices using different seed dispersal values ($f_d = 0.2$, 0.6 and 1.0) and disturbance regimes ($k = 1$, 3 and 5%). The trend followed by λ_M in response to these variables was similar to the results presented in the previous section (Fig. 6.6). However, λ_M was slightly higher under these new conditions, especially when low dispersal values and disturbance regimes were considered. For example, when $k=1\%$ and $f_d= 0.2$, metapopulation growth rate was 0.981 and 0.980 for 1992-93 and 1993-94, respectively, as opposed to 0.962 and 0.961, respectively, in Fig. 6.4; when $k=5\%$ and $f_d= 1$, though, metapopulation growth rate was 1.306 and 0.993 for 1992-93 and 1993-94, respectively, as opposed to 1.305 and 0.981, respectively, under the previous conditions.

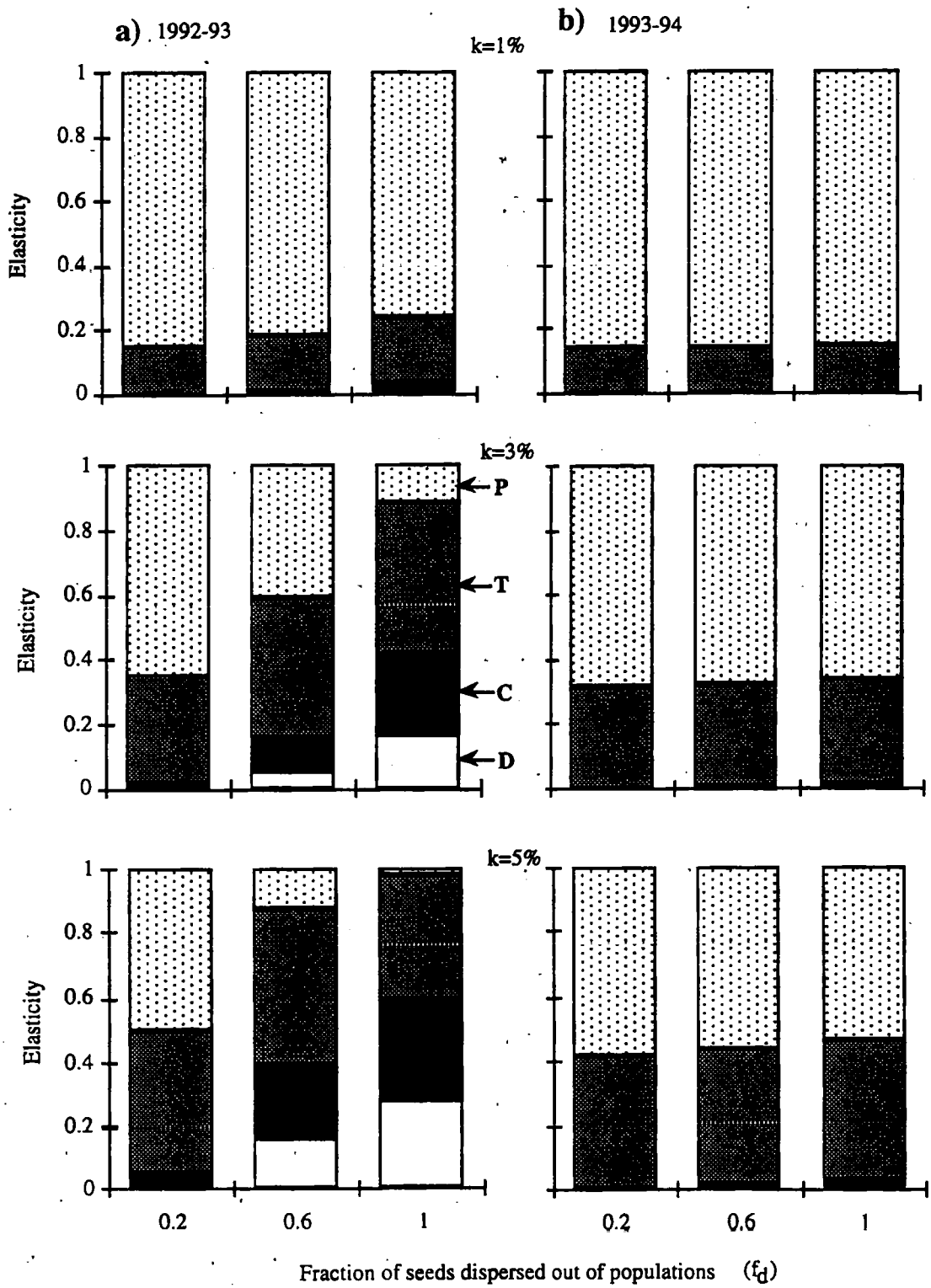
Figure 6.6 Metapopulation growth rate (λ_M) as a function of seed dispersal (f_d) and disturbance regime (k) for the periods a) 1992-93 and b) 1993-94, assuming **time to population extinction of 46 years**. Disturbance regime values are given on the right. Note the different y axis scales between both graphs.



6.3.3 Metapopulation Elasticity Analysis

Elasticity elements were grouped into four basic parameters affecting λ_M: seed dispersal (D, which is a function of local fecundities, proportion of seeds dispersed out of populations and gap formation rate), colonisation (C, which is a function of seed dispersal and canopy closure rate), transitions among population types (T, determined by canopy closure) and persistence of old populations (P, which depends upon disturbance regime and population extinction rate). The relative contribution of each of these parameters to metapopulation growth rate varied with the different disturbance regime values and proportion of seeds dispersed considered (Fig. 6.7). This variation was more noticeable in the 1992-93 than in the 1993-94 results.

Figure 6.7 Elasticity values for matrix elements corresponding to population persistence (P), population transitions (T), colonisation (C), and dispersal (D) for a) 1992-93 and b) 1993-94, using different values of seed dispersal (f_d) and disturbance regime (k).



In both periods, the elasticity values corresponding to transitions among populations increased as the importance of closed canopy population persistence decreased. Total elasticity corresponding to the persistence of type-4 population decreased with increasing proportion of seeds dispersed out of population (i.e., from left to right of Fig. 6.7) and with increasing disturbance regime (i.e., from top to bottom in Fig. 6.7). This implies that when few gaps are opening in the forest and only a few seeds disperse away from populations, the metapopulation largely depends on the persistence of these existing populations.

The relative contribution of colonisation and dispersal to metapopulation growth rate increased with higher proportion of seeds dispersing out of populations and higher disturbance regimes. The similarity in the trends followed by colonisation and dispersal is expected, as colonisation was estimated as a function of dispersal. This trend was apparent both in the 1992-93 and 1993-94 results, though in the latter total elasticity values for these parameters were rather small. The low colonisation and dispersal elasticities in 1993-94 resulted from the low fecundities recorded that period; therefore, metapopulation growth rate was much more dependent on local population transitions and persistence.

6.4 Discussion

Recent demographic studies on spatially-structured plant populations have considered the patch type concept, recognising that local population demography is not static but instead varies in response to environmental change (Martínez-Ramos *et al.* 1985; Olivieri and Gouyon 1985; Horvitz and Schemske 1986; Alvarez-Buylla and García-Barrios 1991; Alvarez-Buylla and García-Barrios 1993; Cipollini *et al.* 1993, 1994; Alvarez-Buylla 1994; Wu and Levin 1994). Some metapopulation studies have used the stochastic approach to address this issue and have modeled the effect of different stochasticity sources on local population extinction (Hanski 1991; Lande 1993; Perry and González-Andujar 1993).

However, the type of environmental variation that many populations experience within plant metapopulations is often the result of directional (i.e., non-stochastic) changes which are part of secondary succession processes. In the case of *P. vulgaris*, the variation in local population demography is determined mainly by changes in canopy cover along the forest regeneration cycle.

In this context, the patch type concept involves the idea of local populations passing through different consecutive stages along an environmental gradient which is determined by successional processes. Thus, the directionality of habitat change enables the projection of the demographic behaviour and fate of local populations within a metapopulation, provided the patterns of environmental variation can be described. Here, knowledge of some canopy dynamics variables and classification of local populations into patch types allowed me to use basic demographic techniques to model metapopulation dynamics. With the use of a stage-based Lefkovitch matrix that incorporated the transitions and contributions among population types, I was able to address specific metapopulation processes (e.g., dispersal, colonisation, extinction) as well as their effects on metapopulation growth rate. This approach has not been used previously to investigate metapopulation issues and offers a good opportunity to test the effect of different variables on metapopulation dynamics.

In this chapter, I investigated the effect of disturbance regime and seed dispersal on metapopulation growth rate. Increasing both variables had a positive, additive effect on metapopulation growth rate: higher disturbance regimes increased the frequency of newly-opened gaps in the environment, and higher seed dispersal levels increased the probability of gap colonisation. This was a direct consequence of the way in which metapopulation matrix parameters were calculated: colonisation was made dependent on the number of seeds arriving at newly-opened gaps, which in turn was modeled as a function of the rate at which new gaps open in the canopy. Also, the probability of persistence of type-4 populations was higher under higher disturbance regimes, as their probability of becoming type-1 populations following gap creation increased with increasing disturbance regime.

Thus, population 'birth' increased and population 'death' decreased with increasing seed dispersal and disturbance regime values.

Other theoretical and empirical studies have emphasised the importance of seed dispersal in the survival and growth of plant metapopulations. Perry and González-Andujar (1993) modeled the behaviour of a hypothetical annual plant and found that dispersal aided metapopulation growth in a spatially heterogeneous environment. Herben *et al.* (1991) showed that spore transport was the primary factor influencing the behaviour of a metapopulation of *Orthodontium lineare*, a moss species that establishes in rotting wood. A metapopulation study on the mistletoe *Phrygilanthus sonorae* illustrated that its distribution pattern on *Bursera* trees could be explained by the patterns of long-distance (off-tree) seed dispersal by birds (Overton 1994).

According to the results of the model presented in this chapter, increased seed dispersal should enhance metapopulation growth rate in the case of *P. vulgaris*. However, the amount of seed dispersal needed to achieve a positive metapopulation growth rate was improbably high. For example, in the 1992-93 period, 100% of seeds had to be dispersed out of populations to produce a positive metapopulation growth rate using a disturbance regime (k) of 2% (Fig. 6.5). Clearly, this does not occur in natural conditions; a large proportion of seeds must remain in their original population. Note, however, that the model accounts for the colonisation of newly-opened gaps by means of seed dispersal only. Alternatively, new populations could be founded through means other than seed dispersal. Although the buried seed bank appears to be quite sparse (Valverde and Silvertown, in press, Appendix A), it could still play a role in the colonisation of gaps. Colonisation could also result from scattered old individuals surviving in isolation under closed canopy conditions. These could be individuals established from exceptional germination under these conditions or, more likely, survivors of past populations that had gone virtually extinct. If a gap opens in the canopy above one of these individuals, a new population could be founded. Thus, the 'rescue effect' concept, i.e., the process by which seed

dispersal may prevent local populations from going extinct (Brown and Kodric-Brown 1977; Hanski 1982b), could be broadened to include longevity and late reproduction as a means of potentially 'rescuing' local populations from extinction. A new term, the "Methusela effect", could be introduced to describe this phenomenon.

Boyd *et al.* (1990) estimated that *P. vulgaris* plants may live between 10 and 30 years. According to the results presented in Chapter 4, canopy turnover rate (i.e. the time lapse between successive gap formations at any one point in the forest) should be between 34.5 (with k=1%) and 18.5 (with k=2%) years; therefore, successive gap formations in the same forest patch could occur within the life span of an individual, thus preventing population extinction. In this chapter I have considered that a type-4 population growing under closed canopy conditions with λ=0.88, would become virtually extinct in 23 years. However, given sufficiently high disturbance regimes, type-4 populations might never go extinct: gap formation may 'rescue' declining populations by recreating environmental conditions adequate for reproduction, germination and establishment.

As shown in Fig. 6.5, positive metapopulation growth rates were favoured by high fecundities (e.g., in 1992-93), seed dispersal and disturbance regimes. Therefore, this would imply that *P. vulgaris* metapopulations would perform better in highly disturbed habitats and when seed dispersal is maximal. However, the model does not consider other factors that may limit metapopulation growth rate under such conditions. For example, seed dispersal must be moderate for local populations to maintain positive growth rates: if all seeds were dispersed away, local populations would be depleted of seeds so no recruitment would be possible (see Chapter 5). Furthermore, *P. vulgaris* performs poorly in highly disturbed environments, apparently because it does not tolerate high competition levels with other species that colonise more open habitats. Thus, a balance must be reached between the factors that enhance metapopulation growth (e.g., high seed dispersal and disturbance regimes) and those which ensure the survival of individual populations (e.g., low seed dispersal and moderate disturbance regimes).

Metapopulation growth rate was also a function of the availability of seeds for dispersal: the difference in metapopulation growth rates between 1992-93 and 1993-94 was mainly a consequence of the lower 1993-94 fecundities (Fig. 6.5, Table 6.2). In addition to this temporal difference in local population dynamics, various other factors could affect the total number of *P. vulgaris* seeds produced in a metapopulation in natural conditions (e.g., total number, size and type of occupied patches within the forest, population density in each patch, and pollinator availability). But a model can only consider a limited number of factors, and as such, it cannot reproduce reality. However, by extracting the most important elements from real systems and examining their relevant interactions, ecological models may be successful in describing a simplified version of natural systems and assessing the role of particular variables affecting them. In this sense, the model presented in this chapter provides a useful tool for analysing metapopulation dynamics, as well as evaluating the importance of several relevant ecological processes. By evaluating the conditions under which colonisations and extinctions may take place, the model also offers the possibility of testing whether a group of local populations may be regarded as a real metapopulation, i.e., whether it exists in a balance between colonisations and extinctions. Chapter 7 discusses this issue further in the light of the results obtained in previous chapters.

Chapter 7. General Discussion

Different aspects of the ecology of *P. vulgaris* have been approached in the preceding pages with the ultimate aim of illustrating that this species forms natural arrays of local populations that function together as metapopulations. The empirical data on population dynamics and canopy change collected during two consecutive growth periods allowed me to build various ecological models, primarily based on matrix analysis, to project the behaviour of different elements of the system and to test theoretically the effect of particular ecological processes (i.e., seed dispersal and forest disturbance regime) on both overall population and metapopulation dynamics. In this context, the present study is an integration of two different scales at which population ecology may be approached, from the local demography perspective to the metapopulation dynamics level; these scales have been analysed through some of the ecological processes that link them together. In this chapter I discuss the main results presented in this thesis as a whole and evaluate their contribution to particular areas of plant ecology.

7.1 Demography and Population Dynamics

The study of plant demography has become a major research subject in plant ecology over the last two decades. Currently, the demography of a large number of plant species has been studied in detail, directed towards the understanding of the ecological basis for evolutionary change, i.e., the every-day action of natural selection reflected in the basic demographic variables: survival, death and reproduction. An early review of the subject attempted to look for demographic patterns among forest herbs (Bierzychudek 1982b). At present, the amount of data available has allowed a much more detailed analysis of the

demographic patterns emerging within species from similar habitats or with common life histories (Silvertown *et al.* 1993), as well as among populations of the same species in different environmental conditions (Silvertown and Franco 1993; Silvertown *et al.* 1995). In this context, the study I carried out on nine populations of *P. vulgaris* (Chapter 3) contributes to the general knowledge of plant species demography, and in particular, to the ecological research on woodland understory herbs in a gradient of environmental conditions within the forest.

There are many common features between the demography of *P. vulgaris* and other woodland herbs. Many of them depend to a certain extent on gap formation for the accomplishment of one or several life cycle phases (Collins *et al.* 1985). In the case of *P. vulgaris*, seed set, seed germination, and seedling emergence and survival are strongly enhanced in canopy gaps (Valverde and Silvertown, in press, Appendix A), which explains the higher population growth rates observed under such conditions. There are significant demographic differences between populations in forest patches with different light availability. In brighter patches population structure is dominated by smaller/younger plants, whereas individuals in the larger size categories are the most common under closed canopy conditions. This suggests that seedling recruitment must be high during the early phases of colonisation following gap formation, but as the canopy closes, populations might persist largely due to the survival of adults (Pitelka *et al.* 1985; Barkham 1992b; Cipollini *et al.* 1993; Hara and Wakahara 1994).

Like *P. vulgaris*, many other forest understory herbs show high elasticity values in life-cycle elements that correspond to survival of large/old individuals (Silvertown *et al.* 1993; Ehrlen 1995). Nevertheless, fecundity and growth elements made a larger contribution to λ in populations under brighter conditions compared to those under the closed canopy. A similar demographic trend has been observed in other plant species when several populations in various successional stages have been studied (Silvertown and Franco 1993).

Though some woodland herbs appear to show rather constant population growth rates in time (Pitelka *et al.* 1985; Hara and Wakahara 1994; Ehrlen 1995) most populations behave differently from year to year (Werner and Caswell 1977; Barkham 1980; Bierzychudek 1982b; Silvertown *et al.* 1993; Horvitz and Schemske 1995). Population growth rates in *P. vulgaris* differed not only spatially but also in time as a result of yearly variation in fecundity and mortality. This variation, that was responsible for significant yearly differences in the behaviour of both the overall population in the forest and the metapopulation, could have been a result of unfavourable weather conditions during the second period (i.e., spring and summer, 1994, were exceptionally hot and dry). Additionally, seedling emergence may be severely reduced by intense seed predation by rodents (Valverde and Silvertown, in press, Appendix A), which may also vary dramatically from year to year (Price and Jenkins 1986; Hulme 1994).

The demographic variation observed in *P. vulgaris* both in time and space (i.e., in forest patches in different light conditions) has been reported for a large number of plant species (Werner and Caswell 1977; Bierzychudek 1982a; Piñero *et al.* 1984; Horvitz and Schemske 1986; Menges 1990; Alvarez-Buylla and García-Barrios, 1991; Cipollini *et al.* 1993, 1994, among others). This stresses the importance of long-term population dynamics studies across the range of environmental conditions in which species occur in order to obtain a more complete picture of demographic patterns in nature.

7.2 Seed Dispersal

Chapter 5 and 6 analysed the theoretical effect of long-distance seed dispersal on overall population growth rate and metapopulation growth rate, respectively. The results of Chapter 5 showed that increased long-distance seed dispersal resulted in a decrease in overall

population growth rate (in terms of the change in number of individuals in the forest as a whole), primarily because it implied a large amount of seeds loss in individual populations.

Horvitz and Schemske (1986) and Cipollini *et al.* (1993) also used empirical demographic data as a starting point to build a similar patch-and-population dynamics model to test the effect of dispersal on overall population growth rate for *Calathea ovandensis* and *Cynoglossum virginianum*, respectively. *Cynoglossum virginianum* is a forest understory herb that grows under the canopy as well as in clearings. According to the model, there was a small positive effect of long-distance seed dispersal on overall population growth rate in this species, which is determined by both enhanced seedling survival under closed canopy conditions and high probability of seeds landing in such closed canopy patches (Cipollini *et al.* 1993). However, in the gap-dependent understory herb *Calathea ovandensis*, long-distance seed dispersal had a negative effect on overall population growth rate due to the high probability of seeds landing in closed canopy (i.e., uncolonisable) conditions (Horvitz and Schemske 1986). The results reported in Chapter 5 for *P. vulgaris* coincide with those reported by Horvitz and Schemske (1986). These are examples of the population dynamics costs of long-distance seed dispersal, which ultimately decreases population fitness due to the high seed mortality risks involved in it (Venable and Brown 1993).

Despite its inherent costs from the individual and population point of view, long-distance seed dispersal has evolved in many species. Murray (1986) has summarised some of its potential advantages in three hypotheses: 1) it reduces density-dependent seed and seedling mortality near the parent; 2) it may result in non-random movement of seeds towards safe sites; and 3) it may allow plants to colonize ephemeral patches away from the original population (Hamilton and May 1977). The latter hypothesis appears particularly important from the metapopulation point of view: long-distance dispersal increases the probability of encountering unoccupied colonisable patches, which determines the survival and persistence of metapopulations. The importance of long-distance seed dispersal in this context has been discussed in both theoretical and empirical studies (Herben *et al.* 1991; Ouborg 1993; Perry

and González-Andujar 1993; Venable and Brown 1993; Overton 1994). In the case of *P. vulgaris*, the results of the model presented in Chapter 6 also support the hypothesis that long-distance seed dispersal may play an important role in metapopulation persistence and growth.

In summary, the importance of seed dispersal may be analysed at several hierarchical levels. At the *individual* level we would be concerned with the way in which the fitness of parent plants increase or decrease due to the dispersal of their seeds (Murray 1986). At the *population* level the main issue would be how dispersal affects mean population fitness, measured by population growth rate (Caswell 1978). And finally, at the *metapopulation* level, the relevant question relates to the role of seed dispersal in metapopulation growth and maintenance. Hamilton and May (1977) have shown that there may be conflicting forces acting at the different levels, i.e., that the evolutionary stable dispersal strategy from the individual point of view could be sub-optimal from the population perspective. Similarly, in species naturally structured as metapopulations the individual and population optimal rates of dispersal may be different from the 'species optimum', which would tend towards the level of dispersal yielding a maximum colonisation rate of available sites (Hanski 1991). The results presented in Chapter 5 and 6 contribute interesting material to the discussion of this later interpretation of the role of seed dispersal in natural systems.

7.3 Metapopulation Dynamics

Since its re-appearance in the past few years, metapopulation theory has been regarded as 'the population ecology paradigm in conservation biology', as it has provided a useful framework for understanding the threats faced by species in fragmented habitats (Hanski 1989). However, there is still some controversy regarding the limited empirical evidence behind the theory and the actual existence of metapopulations in nature (Harrison 1991;

Silvertown 1991). Thus, its usefulness in addressing conservation problems has been questioned (Harrison 1994).

Most metapopulation models and ideas are based on the existence of a balance between local extinctions and colonisations. Harrison (1991) stated that most of the empirical evidence supporting the theory does not fit this metapopulation concept strictly. Instead, she suggests that most studied cases correspond to 1) populations structured in a 'mainland-island' style, in which persistence depends upon the existence of one or more extinction-resistant populations; 2) patchy populations in which dispersal between patches is so high that the system actually works as a single extinction-resistant population; and 3) non-equilibrium metapopulations in which local extinctions occur in the context of a regionwide decline of a species. We have little knowledge on whether species persist in fragmented landscapes due to metapopulation processes, or due to the long-term survival of populations (Hanski *et al.* 1995).

In this context, the question arises as to whether *P. vulgaris* forms real metapopulations or falls into some other category of spatially structured populations. In other words, to what extent does the persistence of the species in a site depend on a balance between colonisations and extinctions, and how important is seed dispersal in connecting populations together. Long term field data on population persistence, colonisation of unoccupied patches, and seed dispersal could offer an answer to these questions. For the moment, the data presented in this thesis and the models built around them do not allow a straight answer. However, some of the points raised in previous chapters enable me to hypothesize about the conditions under which metapopulation processes would be important for this species. Here I consider some of them.

1) Seed dispersal should connect populations together and allow the arrival of seeds at newly-opened gaps for colonisations to occur. If this is so, the results presented in Chapter 6 illustrated that a high proportion of seeds should disperse away from local populations in

order to achieve positive metapopulation growth rates. It is improbable that such a high amount of seed dispersal would occur in natural conditions. Clearly, rodents play a major role in seed removal; between 50 and 60% of seeds are harvested by these animals (Valverde and Silvertown, in press, Appendix A). However, the importance of rodents in transporting seeds among forest patches and the survival probability of those seeds remains obscure (Price and Jenkins 1986). The amount of seed dispersal required for the metapopulation to persist, though, is a function of local fecundities and disturbance regime. Moderate seed dispersal values would be sufficient to ensure the survival of the metapopulation provided that disturbance regime and local fecundities are sufficiently high.

2) If seed dispersal is limited and is not acting as a linking factor between local populations, the system of *P. vulgaris* patches could not be characterised as a metapopulation. However, as discussed in Chapter 6, colonisation of newly-opened patches could occur through means other than seed dispersal, i.e., from the buried seed bank or from isolated old individuals scattered in closed canopy patches (the 'Methusela effect'). Thus, even if the system cannot be characterised as a metapopulation, the colonisation of newly-opened gaps would still remain as an important process in the long-term persistence of the species at a site; in other words, even if seed dispersal does not play a major role in connecting populations together, similar processes to those arising at the metapopulation level could emerge regardless of the colonisation mechanism.

Also, note that the long-term survival of old individuals remaining in isolation in closed canopy conditions, and their potential to become founders of new populations, could offer an hypothesis about the establishment and success of homostyle populations (see Chapter 2, section 2.1.2). Homostyles are self-pollinating, and thus, single isolated individuals would always be able to produce seeds from which to start a new population, whereas seed production in self-incompatible heterostyles would depend on the availability and efficiency of pollinators.

3) The extinction of local populations is a central aspect to metapopulation theory. This extinction-centred view of metapopulations implies that regional persistence depends upon colonisation. However, there is little empirical evidence concerning the importance of local population extinction in this context (Harrison 1991, 1994). In order to regard the studied *P. vulgaris* system as a metapopulation, local populations should eventually go extinct under closed canopy conditions. As discussed in Chapter 6, the extent to which this occurs in natural environments depends on a host of factors (e.g., local population growth rate in closed canopy patches, disturbance regime and turnover rate, longevity of individual plants). Clearly, there are conditions under which local population extinction could occur, i.e., when local population growth rate and disturbance regime are sufficiently low. From this perspective, *P. vulgaris* systems could perhaps resemble non-equilibrium metapopulations as defined by Harrison (1991): those in which extinction occurs as part of an overall regional decline, usually a product of reduction, fragmentation or deterioration of the habitat. In this context, the source of habitat deterioration leading to local population extinction could be the lack of man-made or naturally generated canopy gaps (Menges 1990).

7.3.1 Metapopulations and Conservation Biology

Some of the aspects discussed above have implications for several conservation biology issues. The results of this thesis could give some insight into the potential consequences of habitat fragmentation, deterioration and loss for *P. vulgaris*, as well as other forest understory herbs.

P. vulgaris is a species frequently associated with ancient forests (Peterken 1974). Many ground flora species characteristic of ancient forests are confined to these environments because they have been able to persist only at sites where there has been a long continuity of woodland. Thus, association with ancient woodlands results from their limited ability to

colonise new forest areas as they become available (Spencer 1989). During the present century a large number of ancient woods in Britain have been clear-felled and some of them have been re-planted with conifers (Nau 1987). This implies significant habitat loss for many species. Considering the limited seed dispersal ability of some forest herbs such as *P. vulgaris* (Cahalan and Gliddon 1985), this habitat loss could lead to regional decline and eventual extinction. In fact, this has been one of the factors responsible for the decrease in *P. vulgaris* abundance over the last decades in Britain and Northern Europe (Cahalan and Gliddon 1985; Triest and Hermy 1994).

It has been suggested that increasing habitat fragmentation may lead some species into metapopulation structures (Hanski 1989; Hanski and Gilpin 1991; Harrison 1991; Verboom *et al.* 1991; Harris and Silva-López 1992; Alvarez-Buylla and García-Barrios 1993). In this context, seed dispersal ability, as well as the scale at which it occurs may become critical aspects affecting the regional long-term persistence of species in this kind of fragmented landscape (Harrison 1988). Additionally, other forms of habitat deterioration may become a potential threat for some species. Many woodland understory herbs are favoured by man-made or natural gap creation in the forest canopy; the loss of traditional coppice practices in Britain may lead to a significant decline in their abundance (Barkham 1992a). This condition could turn *P. vulgaris* systems into non-equilibrium metapopulations. When considering what she defined as non-equilibrium metapopulations, Harrison (1991) stated that "...unstable regional extinction-colonisation dynamics may be induced by anthropogenic habitat changes other than outright fragmentation. For example, species dependent on disturbance-generated habitats are sensitive not only to reduction in the amount of the habitat matrix, but also to changes in the disturbance regime. This is the situation for a number of endangered butterflies in Britain and the United States. In Britain, several species requiring sunny openings in woodlands are declining not only due to deforestation, but also to the cessation of traditional forest coppicing, which generates forest clearings". This may also be the case for many gap-dependent forest herbs.

Thus, it appears that *P. vulgaris* may occur in extinction-resistant, spatially-structured populations in habitats with certain levels of disturbance, but may behave as non-equilibrium metapopulations under low disturbance regimes. The answer to the question of whether there exists a positive balance between colonisations and extinctions in the latter situation, rests on the effectiveness of seed dispersal, as well as other colonisation mechanisms, in allowing the occupation of newly-opened gaps.

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Appendices

Appendix A

This section is the manuscript of a paper that is presently in press in Functional Ecology (accepted for publication on the 6th of July, 1995). It presents results that are relevant to the subject of the thesis, some of which have been partially discussed in Chapter 3. It also shows data that was not included in any of the previous chapters. The manuscript's format has been slightly modified to fit thesis standards.

Spatial variation in the seed ecology of a woodland herb (*Primula vulgaris*) in relation to light environment

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Summary.

1 Patches of *Primula vulgaris* occur across a range of light conditions within forests. To understand how light affects the stages of the life cycle involved in reproduction and recruitment, several fecundity-related variables (flower and capsule production, seed set, seed germination, and seedling establishment) were studied in eight populations across a range of light conditions.

2 The mean number of seeds per plant varied greatly, from 7 to 136, and the percentage of seedling establishment varied from 0.4 to 17.2%. These variables, as well as the number of flowers per plant and fecundity were positively correlated with the light conditions.

3 *P. vulgaris* populations establish in newly opened gaps. How this species colonizes new clearings was investigated by looking at seed survival in the soil and seed removal by potential dispersers, in particular rodents and ants.

4 After 14 months in the greenhouse, only three *P. vulgaris* seedlings were observed germinating from 200 soil samples taken from two populations. Germination of retrieved seeds from buried samples was generally lower than 10%. This suggests that only a small number of seeds remain viable in the soil for long periods of time.

5 Seed removal was high in the populations studied (more than 70% in 10 days). Rodents harvested a greater proportion of seeds than ants. Seed dispersal by ants is known to occur within short distances, but rodents may be long-distance dispersers, which may be important for the long-term persistence of *P. vulgaris* in a site because it allows seeds to reach newly opened gaps.

Key Words: fecundity, light environment, seed pool, seed removal,

Primula vulgaris.

Introduction.

Primula vulgaris Huds. is a common element of the ground flora of ancient woodlands in Britain and Northern Europe (Richards 1989). Although it is a shade-tolerant species, growth and reproduction are favoured by relatively open conditions such as canopy gaps (Keith-Lucas 1968). The forest canopy is a dynamic system in which gaps are constantly opening due to natural disturbances like branch or tree falls (Runkle & Yetter 1987). Many woodland herbs colonize these clearings but the changing light conditions as the canopy closes strongly affects their demography (Collins, Dunne & Pickett 1985). Their populations decrease as gaps close and thus their long-term persistence in a forest depends on the creation of new gaps in the canopy (Bierzychudek 1982; Horvitz & Schemske 1986; Cipollini, Whigham & O'Neil 1993).

To understand how forest herbs persist in such dynamic conditions we need information about ecological processes at two different spatial scales: 1) demographic information at the scale of local populations occupying individual gaps, and 2) metapopulation information at the scale of the forest as a whole. In this paper we address the first of these questions in respect of the seed ecology of *Primula vulgaris*. The seed phase of the life cycle is especially important because seeds may be the means by which new gaps are colonized (by dispersal, or from the seed bank) and because seed production may limit population growth.

Although the demography of temperate woodland herbs has been much studied (Bierzychudek 1982; Collins, *et al.* 1985; Kawano *et al.* 1987; Barkham 1992b), relatively little research has focused on the fates of flowers and seeds in natural conditions. Moreover, most studies have ignored the fact that environmental conditions change as the canopy closes. The effect these changes have on the demography of herb populations is unknown, in particular, the way in which different phases of their life cycle are affected as canopy closure proceeds.

Considering the general lack of information concerning the seed ecology of temperate forest herbs, *P. vulgaris* is a relatively well documented species. Studies on germination and growth have demonstrated that light has a strong effect on these processes under controlled conditions (Keith-Lucas 1968; Helliwell 1980). Flower, capsule and seed production in natural populations vary greatly from season to season and seed set depends on the availability of pollinators (Piper, Charlesworth & Charlesworth 1984; Boyd, Silvertown & Tucker 1990). However, natural populations of *P. vulgaris* occur in a wide range of light conditions and no information is available on the effect of canopy dynamics on the reproductive variables of this species, nor on seed germination and seedling emergence across the range of natural light conditions.

The primary aim of this study was to determine how varying light conditions affect the different phases involved in reproduction and recruitment in *P. vulgaris*, which in turn affect the dynamics of populations in the various successional stages of the canopy regeneration cycle. To such end, flower and capsule production, seed set, seed germination, and seedling establishment were studied in eight populations of *P. vulgaris* across a range of different light conditions.

Other aspects of the seed ecology of *P. vulgaris* that have been little studied are seed longevity and seed dispersal. These are particularly relevant when considering spatially structured populations, since they may affect the colonization of new patches. Some authors have suggested that long-term buried seed pools are primarily responsible for the colonization of newly opened gaps by understory herbs (Brown & Oosterhuis 1981; Brown & Warr 1992). However, the importance of both seedling banks and long-distance seed dispersal as potential sources of colonization has been stressed for some gap-dependent species (Alvarez-Buylla & García-Barrios 1991; Beatty 1991). In this study we addressed the question of the colonization strategy of *P. vulgaris* by examining the buried seed pool in two populations, seed survival in the soil, and seed removal rates by potential dispersers, in particular ants and small mammals.

Materials and Methods.

Field work was conducted at Dancers End Nature Reserve, in Buckinghamshire, U.K (Grid Reference SP902096). This area is mainly a forest of *Fagus sylvatica* (beech) and *Fraxinus excelsior* (ash) on a chalky soil (National Vegetation Classification: W8, *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland, with some stands closer to W12, *Fagus sylvatica-Mercurialis perennis* woodland - Rodwell 1991). It has traditionally been managed through coppice cycles of 5 to 10 years, the coppiced species being mainly hazel (*Corylus avellana*) and hawthorn (*Crataegus monogyna*). Important elements of the ground flora are *Primula vulgaris*, *Mercurialis perennis*, *Rubus fruticosus*, and *Hyacinthoides non-scripta*. Within the forest *P. vulgaris* has a patchy distribution. Six populations in different light conditions were chosen for study.

Two additional populations were studied: one in Woburn Wood, a *Quercus rubur* (oak) and *Castanea sativa* (chestnut) forest in Bedfordshire (Grid Reference SP927325), and another one in Salcey Forest, a *Quercus robur* and *Fraxinus excelsior* forest in Northamptonshire (Grid Reference SP814508)

Light measurement:

The diffuse site factor, which is a way of measuring diffuse light, was used to describe the light environment of each population (Mitchell & Whitmore 1993). It was evaluated through the computer image analysis of hemispherical photographs taken during summer 1993. Photographs were analysed using the program Solarcalc 5.41, which calculates diffuse light as a percentage of open sky in the hemispherical photograph (Chazdon & Field 1987). The mean diffuse light of 7 to 15 photographs was used to characterise the light environment of each population.

1. *Seed production:*

In May 1993, the flowers of 20 reproductive plants chose at random were marked in each population. The resulting capsules were collected and their seeds counted.

Fecundity was calculated using two approaches: the 'mechanistic' and the 'empirical' (Menges 1990). Mechanistic fecundity was given by

$$(\text{Mean No. of seeds per plant}) \times \frac{(\%\text{ of seedling emergence})}{100}$$

Seedling emergence was calculated as described in section 2b.

The empirical approach considers the number of reproductive individuals and the number of seedlings emerging in a population the following year. Empirical fecundity was calculated as

$$\frac{(\text{No. of seedlings at } t+1)}{(\text{No. of reprod. plants at } t)}$$

'Empirical' fecundities were calculated in the eight populations studied by counting the number of reproductive individuals and emerging seedlings in areas of 8 to 25m^2 (depending on plant density) for two consecutive years.

2. *Seed Germination in the greenhouse and seedling emergence in the field:*

a) Seed germination: Seeds were collected in 7 populations during July, 1993. Four replicates of 25 seeds per population were set in petri dishes with wet filter paper in a greenhouse. Four other replicates of 25 seeds per population were subjected to a cold pre-treatment (4°C) for eight weeks in damp conditions before placing them in the greenhouse. Seeds were watered as required. Germination was recorded every month for a year, from July 1993 to July 1994.

b) Seedling emergence: Ten 10x10cm quadrats were marked on the ground evenly spaced along a transect in seven populations. In each of five quadrats, 50 seeds were scattered on the ground in July 1993. No seeds were sown in the other five quadrats. The number of seedlings per quadrat was recorded in May, 1994. The number of seedlings in the control quadrats was subtracted from the number of seedlings in the seeded quadrats before calculating the percentage of seedling emergence.

3. *Seed survival in the soil:*

Ten replicates of 50 seeds were buried 5cm deep in nylon bags (0.03mm mesh approx.) in each of four populations in late July, 1993 (DE1, DE2, DE3, and WW). Five bags were retrieved in late April 1994 and the other five in April 1995. Immediately after retrieval seeds were put in petri dishes with filter paper to test for germination in the greenhouse. If only seed coats were found in the bags it was impossible to tell whether they had died or germinated before retrieval. However, this distinction was not important for the purpose of this experiment as, either way, they would not become part of the buried seed pool.

A further viability test was carried out on the seed batch retrieved in April 1995: after retrieved seeds had been in the greenhouse for one month and when no further germination was being recorded, a sub-sample of 40 seeds per population was taken at random from the seeds left to test for potential viability using tetrazolium dye.

In order to examine the seed pool, 100 soil samples were taken in each of two populations at Dancers End (DE2 and DE6, a gap and a closed-canopy population respectively). Samples were collected in early June 1993, before seed shed, to ensure that seeds in the soil were produced the previous year or earlier. Five cm deep samples were taken with a bulb planter (5cm in diameter) evenly spaced along 10 parallel transects of 10m each.

Immediately after collection samples were spread out in plastic trays in a greenhouse. Trays were kept moist from beneath using capillary matting, the edges of which were immersed in water. The soil was disturbed every three months. Seedlings emerging were identified and removed from trays every month for 14 months.

4. *Seed removal:*

a) The effect of deer.

Ten metal mesh cages (50x50x50 cm, 5 x 5 cm mesh) were set in Woburn Wood to protect *P. vulgaris* capsules from deer in April, 1993. Ten control cages were also set without their lids. The number of flowers per cage was counted at the beginning and the number of capsules recorded at the end of the experiment, in July 1993. Plots were chosen at random.

b) The effect of small mammals.

Small cages (30x30x30 cm, 0.5x0.5 cm metal mesh) were used in Woburn Wood to test the effect of small mammals. In late May 1994, 15 cages were set at random into the ground around *P. vulgaris* plants. Another 15 cages were elevated 5cm above the ground with sticks, excluding only larger seed foragers like deer or birds. Capsules on other non-caged plants were also marked and followed as controls. Capsules were counted at the beginning of the experiment, and re-counted in mid-June and finally in mid-July.

c) The effect of ants.

P. vulgaris seeds possess an elaiosome and are harvested by a number of ant species directly from the capsule (Richards 1989). At Dancers End we have observed *Myrmica rubra* harvesting *P. vulgaris* seeds. This ant is abundant in grasslands and only occasionally present in forest. Rodents and other small mammals also harvest *P. vulgaris*. Rodents remove whole capsules leaving only the stalks and occasional capsule remains on the ground; ants harvest the seeds one by one leaving empty capsules.

Thirty open capsules were marked in each of two sites at Dancers End in July 1994: 1) a population in a grassland (DE1) and 2) a population under a large gap in the canopy (DE2). All seeds were removed from capsules and 20 seeds were then replaced in each. Capsules were kept vertical through a stick to prevent the seeds from falling. The number of seeds per capsule was recorded every other day for a week and finally two weeks later.

In order to determine the amount of seed dispersal taking place through means other than ants or small mammals, we followed the seed removal and replacement procedure outlined above for another 20 capsules in the same two populations, but in this case we covered the capsule stalks with tangle-foot (a non-setting glue that traps insects). In previous observations we noted that tangle-foot repelled both ants and small mammals, so this treatment made seeds unavailable to both types of seed foragers. Additionally, an 8m long transect was set in a population in the grassland at Dancers End. By noting the state of the capsules (e.g. open, closed, empty, damaged) of every plant along the transect, we were able to estimate the proportion of seeds following different fates.

Results.

1. *Seed Production:*

Table A.1 summarises the production of flowers, capsules and seeds by plants from different populations. There was wide variation in all variables. The mean number of flowers produced by plants ranged from 3.7 to 15.1 and the percentage that became capsules ranged from 16.8% to 46.7%. The mean number of seeds per plant (7 to 137) represented almost a 20-fold variation.

Table A.1. Mean flower, capsule and seed production by plants from eight populations of *Primula vulgaris* in three forests. Standard deviations are given in parenthesis. Mean 'mechanistic' and 'empirical' fecundities are also reported. The bottom row refers to the results of the correlations of each variable with diffuse light, given in the first column (% canopy openness). DE1 population was excluded from these analyses because of its different environmental conditions. Percentages were arcsin transformed for normality.

Pop.	Diffuse Light	Flowers per plant	Capsules per plant	% Flowers producing capsules	No. of Seeds per capsule	No. of Seeds per plant	% Seedling Emergence	'Mech.' Fec. (93-94)	'Emp.' Fec. (92-93)	'Emp.' Fec. (93-94)
DE1	93.5	8.8 (4.4)	4.5 (3.7)	46.7 (16.9)	37.4 (18.9)	136.6 (123.4)	4.8	6.6	7.2	2.1
DE2	9.1	8.7 (4.8)	3.1 (3.0)	38.1 (29.2)	35.6 (20.8)	112.1 (129.5)	17.2	19.3	26.9	8.0
DE5	4.9	7.3 (5.4)	1.8 (1.7)	26.3 (21.4)	35.0 (17.8)	63.0 (75.4)	6.0	3.8	10.8	0.7
WW	4.8	3.8 (2.6)	0.8 (0.8)	21.8 (26.5)	41.7 (18.3)	31.2 (35.4)	2.8	0.9	0.3	0.3
SF	3.1	15.1 (11.7)	2.7 (3.6)	16.8 (16.9)	24.4 (23.6)	65.5 (98.8)	0.4	0.3	0.1	0.2
DE4	1.9	-	-	-	-	-	2.0	-	0.8	0.2
DE3	1.9	5 (2.8)	1.0 (1.1)	24.8 (23.8)	34.9 (27.8)	36.8 (54.0)	2.8	1.0	0.3	0.5
DE6	1.6	4.2 (2.6)	0.7 (0.8)	19.5 (21.2)	9.5 (10.4)	7.5 (12.5)	-	-	0.5	-
		R^2=0.03 p=0.76	R^2=0.43 p=0.15	R^2= 0.71 p=0.03	R^2=0.29 p=0.27	R^2= 0.72 p=0.03	R^2= 0.84 p= 0.01	R^2= 0.83 p= 0.01	R^2= 0.83 p= 0.004	R^2= 0.78 p= 0.02

The number of flowers per plant was not correlated with the light conditions at each site. However, both the percentage of flowers that produced capsules and number of seeds per plant showed a significant correlation with diffuse light (Table A.1).

The mean number of seeds that each plant produced was significantly correlated with its initial number of flowers (data not shown), though the correlation was not very strong (both variables Log transformed, R^2= 0.24, p<0.0001, d.f.= 138). None of the variables presented in Table A.1 shows any significant difference between pin and thrum flower morphs (according to paired *t*-tests- data not shown).

The 'empirical' fecundity estimates (Table A.1) differ widely for the two periods analysed. For the period 1993-94, fecundity was also calculated using the 'mechanistic' approach. This resulted in consistently greater estimates of fecundity than with the 'empirical' approach. However, regardless of the calculation method, fecundity and light conditions were positively correlated.

2. *Seed germination in the greenhouse and seedling emergence in the field:*

Table A.2 summarises seed germination in the greenhouse after 14 months in all seven populations. Seeds germinated at an approximately constant rate, although there was a slight peak around February 1994, the time when seedling emergence occurs in natural conditions. Final germination was similar in both non-pretreated and cold-treated seeds.

Germination velocity was measured by the variable t_{50}, the time needed to achieve 50% germination (Grime, *et al.* 1981). A MANOVA was performed to test the effect of pre-treatment and of individual population conditions on the two variables (final germination - arcsin transformed for linearity - and t_{50}). The results indicated that final germination was significantly affected by population (F=20.95, p<0.0001), but not by pre-treatment (F=1.64, p=0.206). However, both pre-treatment and population significantly affected germination velocity (F=26.23, p<0.0001 and F=11.88, p<0.0001 respectively). Seeds subjected to the cold pre-treatment germinated faster that non-pre-treated seeds and seeds

from Salcey Forest showed a significantly lower final germination than the other populations.

Table A.2. Final germination percentage after one year and germination velocity (measured by the variable t_{50}) for *P. vulgaris* seeds from seven populations. Values sharing the same letter do not differ significantly within columns according to a Tukey-Kramer test performed after a MANOVA.

Population	% Final Germination (non pre-treated)	t 50 (non- pre-treated)	% Final Germination (cold pre-treatment)	t 50 (cold pre-treatment)
DE1	95 a	164.25 b	99 a	87.7 b
DE2	97 a	154.0 bc	84 a	123.5 ab
DE3	92 a	105.0 ac	87 a	99.5 bc
DE5	90 a	112.75 ac	91 a	94.2 b
DE7	93 a	102.0 a	87 a	86.0 b
WW	90 a	186.0 b	90 a	133.5 ac
SF	58 b	170.67 b	58 b	156.3 a

Seedling emergence was positively correlated with diffuse light, varying from 0.4% in a population under the canopy, to 17.2% in the population in a gap (see Table A.1).

3. *Seed Survival in the Soil:*

When we retrieved the buried seed bags, we found a varying number of empty seed coats suggesting that germination (or death) occurred long before retrieval. In both years little germination was recorded when seeds were put in the greenhouse after the period of burial (Table A.3). Germination percentage after retrieval exceeded 10% only in two cases. Seeds that germinated did so during the month following retrieval.

The results of the tetrazolium test and observations on seed germination after retrieval, as well as on the number of retrieved seeds that appeared sound, indicated that, from the total number of seeds originally buried in July, 1993, only 9.8%, 19.8%, 25% and 13.6% (for DE1, DE2, DE3 and WW, respectively) were still alive after 21 months.

Table A.3. Mean number of seeds germinated in the seed burial/retrieval experiment. Figures were obtained as averages of seed germination from 5 samples of 50 seeds buried in each population. Numbers in parenthesis indicate standard deviations.

Population	Mean no. of seeds germinating after retrieval	% germination after retrieval
	Seeds retrieved in May, 1994	
DE1	0.25 (0.5)	0.5%
DE2	1.25 (0.96)	2.5%
WW	11.50 (4.43)	23%
DE3	3.25 (0.96)	6.5%
	Seeds retrieved in May, 1995	
DE1	1.33 (0.58)	2.7%
DE2	4.25 (2.63)	8.5%
WW	5 (8.66)	10%
DE3	6.6 (5.45)	13.2%

Only three *P. vulgaris* seedlings were observed (during April 1994) germinating from the buried seed pool in the two populations at Dancers End. All of them were in the soil samples collected from the population in the gap, where plant density is much higher. Germination conditions were good, as seeds of other species germinated in the samples during the course of the experiment.

4. *Seed removal:*

a) The effect of deer.

Of all the flowers counted inside the cages at the beginning of the experiment, 3.25% survived as capsules in control cages and 5.97% in deer exclusion cages. The number of capsules that survived in both treatments was not significantly different according to a G test performed on capsule counts ($G=3.81$, $p>0.05$, d.f.= 1).

b) The effect of small mammals.

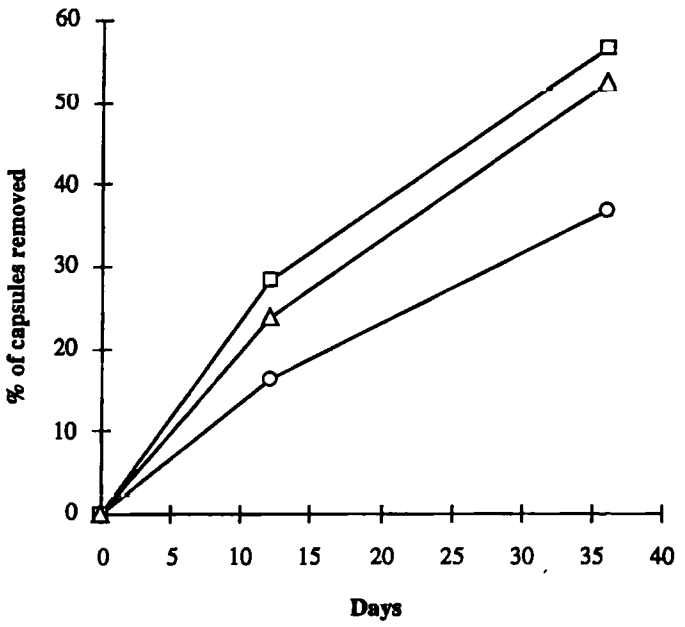
The effect of the three treatments (large and small mammals excluded, only large mammals excluded, and controls) was analysed through a multiple G test (Table A.4), which indicated that the treatments had a significant effect on the number of capsules removed ($G= 6.62$, $p<0.05$, d.f.=2).

Table A.4. Capsule removal in Woburn Wood. Values sharing the same letter in the last column do not differ significantly according to a paired G tests.

Treatment	No. of capsules remaining	No. of capsules removed	Proportion removed
Large and small mammals excluded	46	27	0.369a
Only big mammals excluded	38	50	0.568b
Control (no exclusion)	18	20	0.526b

Figure A.1 shows the capsule removal rate in this experiment. After twelve days the proportions of capsules missing in both, the large mammals exclusions and the control plants, were already higher than in the total exclusion treatment, though not significantly different from it. After 36 days the number of missing capsules was significantly higher in the large mammals exclusions and in the control plants than in the total exclusions (Table A.4). Roting was responsible for some capsule loss, which also explains the high proportion of capsule loss in the total exclusions.

Figure A.1. Capsule removal rate at Woburn Wood during June/July, 1994. Circles: total exclusions; squares: only large mammals excluded; triangles: controls (no exclusions).



c) The effect of ants.

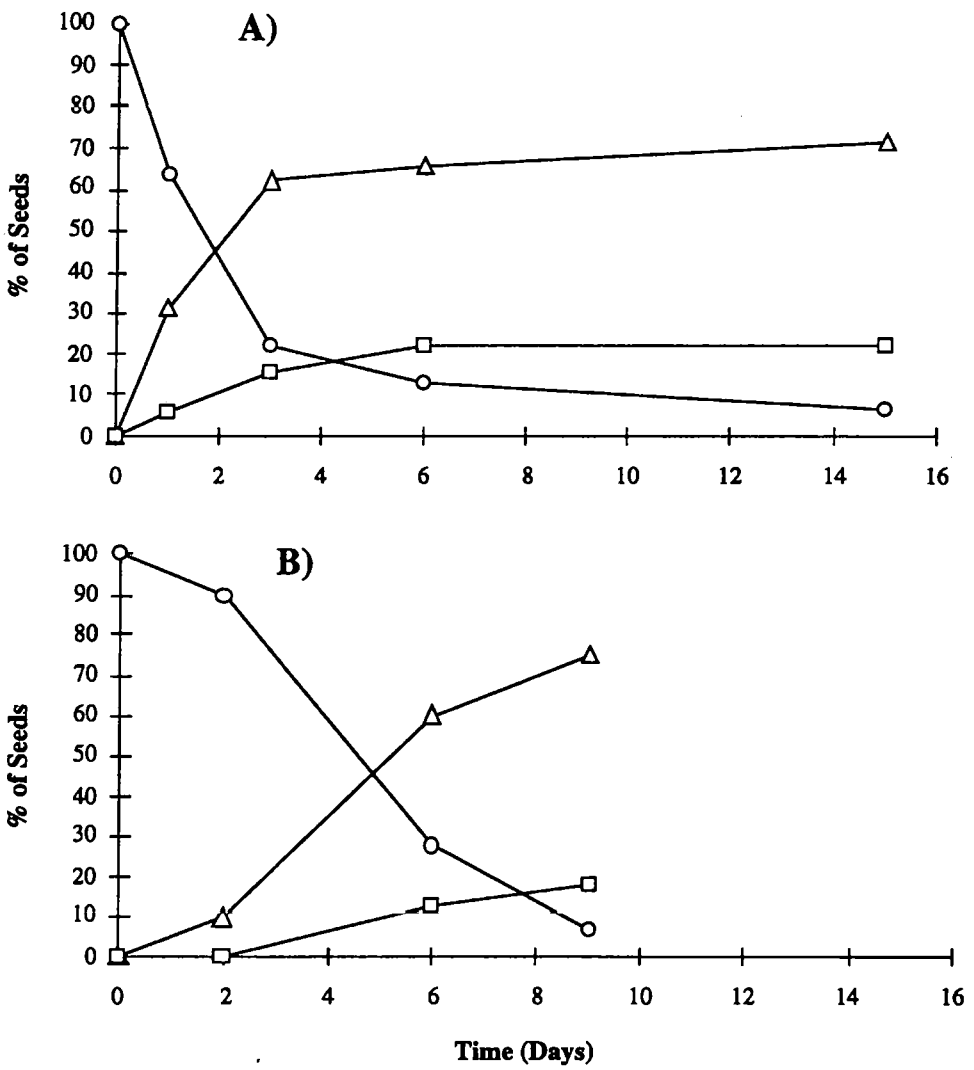
Figure A.2 shows seed removal rate from populations DE2 and DE1. Only around 10% of the seeds were left after 9 and 15 days respectively. As ants leave empty capsules and rodents harvest the whole capsule leaving only the stalks, we were able to estimate seed removal by both ants and rodents. Most seed loss was due to rodent activity in both populations and seeds were removed at a faster rate in the population in the grassland as compared with the population in the gap.

However, in the experiment where the capsule stalks were covered with tangle-foot we found that 41.3% (after 15 days in DE1) and 36.7% (after 9 days in DE2) of the seeds were lost from capsules, regardless of the tangle-foot and of the fact that they were kept in a vertical position. This suggests that seed removal was overestimated in the previous experiment, especially regarding ant activity, as capsules can be found empty as a result of seed removal by ants and/or random seed dispersal.

From a sample of 173 capsules recorded along an 8m transect in the population at the grassland, 59.8% had signs of rodent activity, while only 17.4% had signs of ant activity or

dispersal at random (undamaged capsules were found empty or semi-empty). Other capsules were still closed and only 7.5% of them appeared open but still un-touched. These results are similar to the proportions of ant-removed, rodent-removed and non-removed seeds shown in both graphs in Fig. A.2.

Figure A.2. Removal of *P. vulgaris* seeds by ants and rodents in a population in A) a grassland, and B) a gap at Dancers End Reserve during summer, 1994. Circles: seeds left; triangles: seeds removed by rodents; squares: seeds removed by ants.



Discussion.

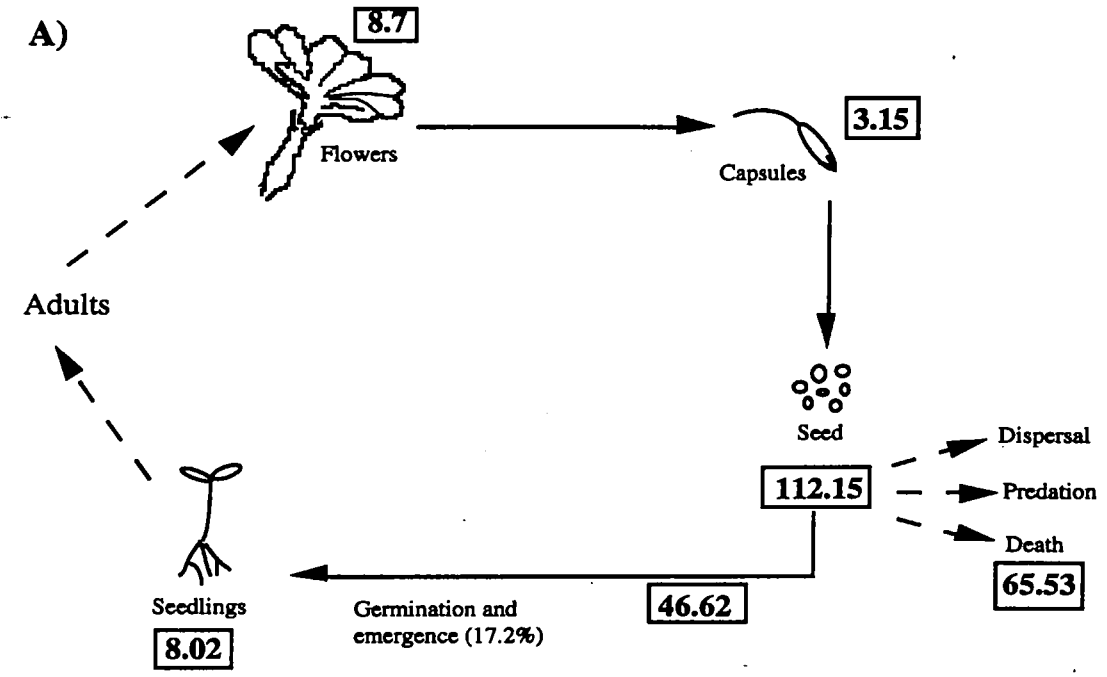
Although *P. vulgaris* has been characterised as a shade-tolerator (Keith-Lucas 1968), our results have shown that most measures of reproductive output were enhanced under brighter

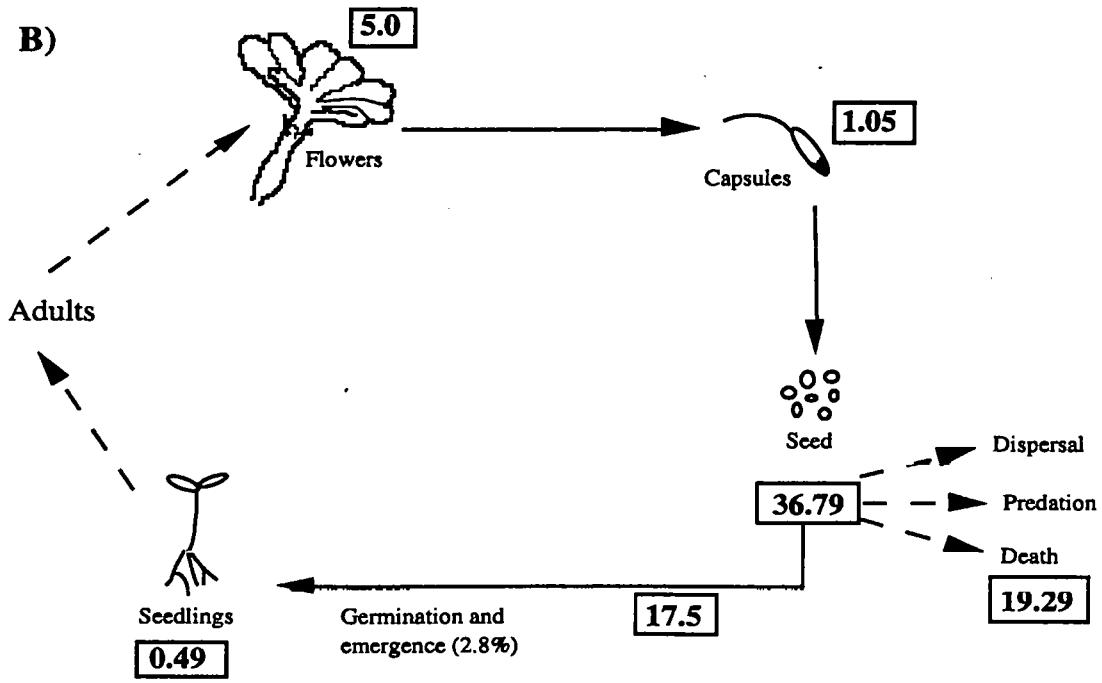
conditions. This must have a dramatic effect on the demography of populations established in patches with varying light availability. As a matter of fact, population growth rates are positive in canopy gaps and negative under closed canopy (T. Valverde, unpublished data). This has also been observed for other gap-dependent woodland herbs, such as *Cynoglossum virginianum* (Cipollini, *et al.* 1993) and *Calathea ovandensis* (Horvitz & Schemske 1986). The demographic change caused by canopy closure in these species was the result of a decrease in fecundity-related parameters, as seems to be the case for *P. vulgaris*.

The comparison between the reproductive variables measured in two of the studied populations in contrasting light environments provides detail regarding the specific transitions that may be affected during the process of canopy closure (Figure A.3). Although the number of flowers per plant was similar in both populations the final fecundities differed more than 15-fold. Most of the variation in final fecundity values was caused by a dramatic decrease in the percentage of flowers producing capsules and in seedling emergence under darker conditions. As capsule production in this species appears to be related to pollinator availability (Piper, *et al.* 1984; Boyd, *et al.* 1990), the spatial variation in capsule production between populations suggests that there might be light-related differences in pollinator abundance in different forest patches.

With regard to the variation in seedling emergence, our results suggest that recruitment is high during the establishment of populations following the opening of gaps, but very low after canopy closure. This raises the question of how *P. vulgaris* persists through forest regeneration cycle. New populations may colonize canopy gaps in three ways: 1) through the re-initiation of population growth from old individuals that have survived for long periods under a closed canopy, 2) through seed germination from a long-term seed pool, or 3) through seeds reaching gaps by means of seed dispersal. The results presented in this paper allow us to evaluate the likelihood of the two latter mechanisms of population re-establishment.

Figure A.3. Different phases of the reproductive cycle of *P. vulgaris* in A) a population in a gap (DE2), and B) a population under closed canopy conditions (DE3). The figures in the squares are the per plant averages as reported in Table A.1. The number of seedlings are given by the 'empirical' fecundities for 1993-94. The number of seeds leaving the population (through dispersal, predation or death) was calculated using other measured and reported variables (empirical fecundity, % of seedling emergence and no. of seeds per plant - see text).





It appears that the majority of *P. vulgaris* seedlings recruited in a population during a given season come from the previous year's seed production rather than from a long-lived seed pool. We found only a small number of *P. vulgaris* seedlings in the soil samples that we analysed, which coincides with what other studies have reported for this species (Brown & Oosterhuis, 1981; Brown & Warr 1992; Warr, Kent & Thompson 1994). Furthermore, we obtained generally low germination percentages in seeds that had been buried for 9 and 21 months, which is in agreement with the results of Boyd *et al.* (1990), who observed that most *P. vulgaris* seeds found in the soil failed to germinate in greenhouse conditions.

Germination in seed samples within the bags buried in the soil in our experiment (as shown by the presence of empty seed coats) followed an almost 'all-or-nothing' pattern, which might have been related to relative humidity or other local micro-environmental conditions at the burial site. This suggests that there is no long-term seed dormancy, which is also supported by the high germination percentages we obtained in the greenhouse. Keith-Lucas (1968) and Helliwell (1980) found that *P. vulgaris* seeds lose their viability after 9 months of dry storage. Although our results show that this does not occur in natural conditions, since the tetrazolium test indicated that between 10% and 25% of the seeds buried can actually remain alive for at least 21 months, the germination capacity of older seeds does seem to be limited.

With regard to seed dispersal as a mechanism for colonization of newly opened gaps, our results suggest that ants harvested only a small proportion of seeds. Moreover, they generally disperse *P. vulgaris* seeds within centimetres from the source (Keith-Lucas 1968). In a study of genetic neighbourhood size Cahalan and Gliddon (1985) reported that in the absence of ant dispersal, most seeds landed a few centimetres away from the capsule.

The arrival of dispersed seed in gaps must occur through exceptional long-distance dispersal by ants or through other dispersal vectors, among which rodents are probably the most important. Richards (1989) reported that *P. vulgaris* seedlings are common outside the burrows of mice and voles, which suggests that these animals may act as seed dispersers as well as seed consumers. Some rodents from temperate habitats have been reported to store

between one third and one fifth of their harvest (Price & Jenkins 1986). Nevertheless, rodent foraging and feeding behaviour may vary greatly in space and time with seed density, rodent abundance, weather conditions and the availability of other food sources (Hulme 1994). Long-term estimates of their effect as seed consumers/dispersers are unavailable.

The comparison between 'mechanistic' and 'empirical' fecundities offered a further estimate of seed loss in the populations studied. 'Mechanistic' fecundities were consistently higher than 'empirical' fecundities (Table A.1). To calculate the former, we considered the percentage of emerging seedlings from a sample of seeds sown in the field, together with the data on seed production. The difference between the two estimates may be explained by seed removal, that was avoided to some extent in the 'mechanistic' method by sowing the seeds directly into the soil, but was implicit in the results of the 'empirical' fecundities.

Figure A.3 illustrates different phases of the reproductive cycle of *P. vulgaris* with the average numbers *per plant* entering each phase in two populations for the period 1993-94. 'Empirical' fecundities were used as a measure of the number of seedlings emerging in 1994 per reproductive plant in 1993. The number of seeds leaving each population as a result of either long distance dispersal, predation or death was calculated as:

$$\text{Seeds leaving} = (\text{No. of seeds/plant}) - \frac{(\text{Empirical Fecundity}) \times 100}{\% \text{ of seedling emergence}}$$

According to these calculations, 58% (65 out of 112 seeds per plant) and 52% (19 out of 37 seed per plant) of the seeds produced in populations DE2 and DE3, respectively, were lost. These percentages are strikingly similar, despite the differences in environmental conditions, plant density, and seed abundance between the two populations. Our other observations on seed removal (as described in Fig. A.1 and the transect results in section 4c) also gave very similar estimates. These data indicate that seed removal plays a major role in decreasing seedling recruitment in natural populations under various light conditions. The fate of those seeds and their role in colonising newly open gaps remain to be investigated.

The long-term persistence of *P. vulgaris* at a site depends on the opening of areas for potential colonisation through either natural disturbances or coppicing. After gap formation

new populations may potentially become established from isolated scattered individuals within the forest, or less likely, from seeds buried in the soil. Besides this, gap colonisation through seed dispersal from adjacent populations may also play a critical role. Local extinction could occur if seed dispersal sources (i.e. forest patches occupied by *P. vulgaris* populations) are scarce and isolated. This has important implications for forest management, particularly if dispersal is important. The gradual loss of traditional coppicing practices in a great number of ancient woodlands in Britain could lead to a decrease in the species abundance by reducing the number of colonisable patches (Barkham 1992a).

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Appendix B.1

The aim of the log-linear analysis performed in Chapter 3 was to determine the significance of the effect of time (years) and forest patch (population) on population structure and transition matrices. In the case of the observed population structure, the data formed a three-way contingency table in which the explanatory variables were year (1992, 1993 and 1994) and patch (DE1, DE2, DE3, etc.), and the response variable was frequency of individuals per stage category. In the case of entire transition matrices the data formed a four-way contingency table in which the explanatory variables were year (1992-93 and 1993-94), patch (DE1, DE2, DE3, etc.), and initial category (seedling, juvenile, adult 1, etc.), whereas the response variable was the frequency of individuals that followed each fate (juvenile, adult 1, death, etc.).

In a log-linear analysis a frequency table is described by a model which gives the logarithm of the cell frequencies as a linear function of the factors defining the table and their interactions. To test the effect of the different factors (or in this case, the degree of independence between them), several hierarchical models are considered, in which the presence of an interaction between two or more factors implies the presence of all lower order interactions that include the factors in question. How well a particular log-linear model fits the data is measured by χ^2. The significance of an interaction between two or more factors is analysed by examining the reduction in χ^2 when the interaction is added to a model that excludes it.

Thus, for instance, to find out the significance of the effect of *initial category*, *patch* and *year* on the *fate* of individuals (Table b below), the null hypothesis was that the *fate* of individuals was independent of *patch* and *year*, only conditional on *initial category*. In the corresponding log-linear analysis the FY (*fate-year*) and FP (*fate-patch*) interactions were excluded, together with all the higher order interactions that involved those terms (FIY, FIP,

FYP, FIYP). The null hypothesis (IPY, FI) failed to fit; thus, it was concluded that *fate* was significantly affected by *year*, *patch*, or both. To analyse the effect of *year*, factor Y was added and the model IPY, FIY was tested. It did not fit either, so *year* was not responsible for the lack of fit of IPY, FI. However, adding Y to the FI interaction reduced X^2 by 284.59, an amount that is significant at $p<0.001$; thus, it was concluded that the effect of *year* on *fate* was significant (Caswell 1989).

The same procedure was followed to test the significance of the effect of *patch* and it was concluded that it significantly affected the *fate* of individuals as well. If both, *patch* and *year* affect *fate*, they may or may not interact. If the model IPY, FIY, FIP fits the data, it can be concluded that both *patch* and *year* have an effect on *fate*, but their effects are separable. In the case of Table b below, the model with the three three-way interactions did not fit either, which means that the factors *patch* and *year* interact in their effect on *fate*. Because the effect of an interaction is always measured in relation to a specified model, there are several ways to measure the significance of an interaction. The tables below report two different ways of measuring the effect of the explanatory factors on the response variable (Silva *et al.* 1990).

If the explanatory factors are not independent of each other, it is interesting to look at the interaction between two of the factors within each level of a third factor (Sokal and Rohlf 1981). This was done by testing the effect of *initial category* and *patch* on the *fate* of individuals for each of the two *years* studied (1992-93 and 1993-94), and by examining the effect of *year* and *patch* on the *fate* of individuals within each *initial category*. The results are shown in the tables below.

a) Results of the log-linear analysis for the models of **observed population structures** (frequency of individuals in each category) for **three years** in **nine** *P. vulgaris* populations. Structural zeros were included in some cells in populations DE1, DE6 and DE7 (DE6 and DE7 data was available for only two years and DE1 is sub-divided in only four stage categories). A constant 0.5 was added to all cells prior to analysis (Silva *et al.* 1990). Symbols are as follows: P = patch (DE2, DE5, DE3, etc.); Y = year (1992, 1993 and 1994); C = category (seedling, juvenile, adult 1, adult 2 and adult 3).

Model	Effect	*d.f.*	X^2	ΔX^2	p
PY, C		91	1133.76		<0.001
PY, CY		83	905.39		<0.001
	Year	8		228.37	<0.001
PY, CP		59	412.33		<0.001
	Patch	32		721.43	<0.001
PY, CP, CY		51	112.74		<0.001
	Year	8		399.59	<0.001
	Patch	32		892.65	<0.001
PYC		0	0		1.0
	Year x Patch	51		122.74	<0.001

b) Results of the log-linear analysis for the models built with **entire transition matrices** from **nine** *P. vulgaris* populations, for the periods **1992-93** and **1993-94**. Frequency matrices (like Table 3.2, with death as a fate and no fecundities) were used for the analysis. Structural zeros were included in some cells in populations DE1, DE6 and DE7 (see details in previous table). A constant 0.5 was added to all cells prior to analysis (Silva *et al.* 1990). Symbols are as follows: P = patch (DE2, DE5, etc.); Y = year (1992-93 and 1993-94); I = initial category (seedling, juvenile, adult 1, etc.); and F = fate (death, juvenile, adult 1, etc.).

Model	Effect	*d.f.*	X^2	ΔX^2	p
IPY, FI		272	1119.39		<0.001
IPY, FIY		252	834.80		<0.001
	Year	20		284.59	<0.001
IPY, FIP		112	407.25		<0.001
	Patch	160		712.14	<0.001
IPY, FIY, FIP		92	196.43		<0.001
	Year	20		210.82	<0.001
	Patch	160		638.37	<0.001
IPYF		0	0		1.0
	Year x Patch	92		196.43	<0.001

c) Results of the log-linear analysis for the models built with **entire transition matrices** from eight *P. vulgaris* populations, **for each of two periods** (1992-93 and 1993-94). Symbols and other details of the analysis as detailed in Table b).

1992-93

Model	Effect	*d.f.*	X^2	ΔX^2	p
PI, F		147	2576.58		<0.001
PI, FP		119	1916.57		<0.001
	Patch	28		660.01	<0.001
PI, FI		131	479.28		<0.001
	Initial Category	16		209.73	<0.001
PI, FP, FI		103	118.72		0.138
	Patch	28		360.56	<0.001
	Initial Category	16		1797.85	<0.001
PIF		0	0		1.0
	Patch x Init. Categ.	103		196.43	0.138

1993-94

Model	Effect	*d.f.*	X^2	ΔX^2	p
PI, F		147	3433.55		<0.001
PI, FP		119	2928.83		<0.001
	Patch	28		504.72	<0.001
PI, FI		131	315.90		<0.001
	Initial Category	16		3117.65	<0.001
PI, FP, FI		103	137.92		0.012
	Patch	28		177.98	<0.001
	Initial Category	16		2790.91	<0.001
PIF		0	0		1.0
	Patch x Init. Categ.	103		137.92	0.012

d) Results of the log-linear analysis for the correspondent models of **each of the initial categories** for the frequency matrices from **nine** *P. vulgaris* populations, **for 1992-93 and 1993-94.** Symbols and other details of the analysis as detailed in table b).

Initial Category:
Seedlings

Model	Effect	*d.f.*	X^2	ΔX^2	p
PY, F		56	229.44		<0.001
PY, FY		52	168.15		<0.001
	Year	4		61.29	<0.001
PY, FP		24	75.50		<0.001
	Patch	32		153.94	<0.001
PY, FY, FP		20	30.49		0.062
	Year	4		45.01	<0.001
	Patch	32		137.65	<0.001
PYF		0	0		1.0
	Year x Patch	20		30.49	0.062

Initial Category:
Juveniles

Model	Effect	*d.f.*	X^2	ΔX^2	p
PY, F		56	188.43		<0.001
PY, FY		52	106.43		<0.001
	Year	4		82.0	<0.001
PY, FP		24	80.07		<0.001
	Patch	32		108.36	<0.001
PY, FY, FP		20	18.64		0.545
	Year	4		61.43	<0.001
	Patch	32		87.79	<0.001
PYF		0	0		1.0
	Year x Patch	20		18.64	0.545

Initial Category: **Adults 1** Model	Effect	*d.f.*	X^2	ΔX^2	p
PY, F		56	385.01		<0.001
PY, FY		52	279.81		<0.001
	Year	4		105.20	<0.001
PY, FP		24	153.49		<0.001
	Patch	32		231.52	<0.001
PY, FY, FP		20	86.41		<0.001
	Year	4		67.08	<0.001
	Patch	32		193.40	<0.001
PYF		0	0		1.0
	Year x Patch	20		86.41	<0.001

Initial Category: **Adults 2** Model	Effect	*d.f.*	X^2	ΔX^2	p
PY, F		56	271.73		<0.001
PY, FY		52	228.20		<0.001
	Year	4		43.53	<0.001
PY, FP		24	92.14		<0.001
	Patch	32		179.59	<0.001
PY, FY, FP		20	50.43		0.001
	Year	4		41.71	<0.001
	Patch	32		177.77	<0.001
PYF		0	0		1.0
	Year x Patch	20		86.41	0.001

Initial Category: **Adults 3** Model	Effect	*d.f.*	X^2	ΔX^2	p
PY, F		48	84.85		<0.001
PY, FY		44	74.13		<0.001
	Year	4		10.72	<0.05
PY, FP		16	27.34		<0.001
	Patch	32		57.51	<0.005
PY, FY, FP		12	19.81		0.071
	Year	4		7.53	<0.5
	Patch	32		54.32	<0.01
PYF		0	0		1.0
	Year x Patch	12		86.41	0.071

Appendix B.2

Statistical results of the comparison of population structures using the log likelihood ratio. The Table below gives the G values obtained in each comparison calculated as detailed in section 3.2. The critical value of G (95%) is 7.81 for 3 degrees of freedom (d.f.) and 9.49 for 4 d.f.. Population structures were considered significantly different when the obtained G was larger than the critical value at 95%; comparisons that resulted *not significant* are given in bold figures.

	Observed in 1993 vs. Stable 1992-93	Observed in 1994 vs. Stable 1993-94	Observed in 1993 vs. observed in 1994	Stable 1992-93 vs. stable 1993-94
DE1 (d.f. = 3)	281.27	96.57	194.85	13.58
DE7 (d.f.=4)	—	19.06	—	—
DE2 (d.f.=4)	1315.07	146.62	476.56	**6.09**
DE5 (d.f.=4)	600.31	**1.89**	3352.82	111.29
WW (d.f.=4)	20.63	86.94	16.44	**7.42**
SF (d.f.=4)	32.51	**2.33**	**9.35**	20.48
DE3 (d.f.=4)	40.21	44.65	34.80	57.51
DE4 (d.f.=4)	12.21	19.79	161.81	71.05
DE6 (d.f.=4)	10.21	—	—	—

Appendix C.1

Chapter 5 presented a model that included population dynamics in specific patch-types along the forest regeneration cycle, as well as patch dynamics given by the changes in the forest canopy, to describe the way in which overall numbers of *P. vulgaris* individuals change in time at a site. In order to describe patch-specific demography for the periods 1992-93 and 1993-94, I chose the projection matrices obtained directly from the populations studied in patches with different light conditions, corresponding to the various patch-types defined. In some cases empirical data from two populations with similar diffuse light were pooled to obtain new transition probabilities and build a projection matrix that reflected in a more accurate way the behaviour of an hypothetical population under that particular range of light conditions (Table 5.2).

A different approach was also attempted in order to built hypothetical patch-specific population matrices based on the empirical data available. In this appendix I present some preliminary results of these approach, as well as the reasons why I preferred the criteria applied in Chapter 5.

As there is a strong relationship between population growth rate (λ) and light conditions (Fig. 3.3), I assumed there was also a relationship between each specific matrix entry and diffuse light. Thus, I defined a simple linear function describing the relationship between matrix element $a_{i,j}$ and the range of light conditions for which it was empirically calculated. I obtained the value of that particular matrix element for an hypothetical population under x% canopy openness as follows

$$a_{i,j} = m\,(x\%) + b \qquad (1)$$

where m and b are the slope and the y intercept, respectively, of a linear regression between empirically calculated $a_{i,j}$ and light conditions, as given by the entire data set from 1992-93

and 1993-94 periods. Transitions from each particular initial stage to all possible fates, including death (angular transformed), as well as fecundity entries were considered.

New matrix elements and stage-specific mortalities were calculated for four hypothetical populations under 12%, 6%, 3% and 1.5% canopy openness, in order to build projection matrices for type-1, 2, 3, and 4 patches, respectively, as defined in Table 4.2. In each case, the calculated probabilities of each initial stage contributing to all possible fates (including death) were standardize to sum to unity. The example that follows illustrates the calculation of the first column of a projection matrix for an hypothetical type-1 population (12% canopy openness):

The first column of the matrix in question involves the calculations of the following transitions: seedlings-to-juveniles, seedlings-to-adult 1, and seedlings-to-'death', which together must sum to unity. The relationship between the seedling-to-juvenile transition and diffuse light is given by the function $y = 1.185\ (x) + 0.321$ (both variables angular transformed - Fig. C.1). In an hypothetical population under 12% canopy openness, the expected transition probability from seedlings to juveniles was calculated as follows:

Angular transformation of hypothetical light value: $x = \arcsin(\sqrt{12}) = 0.354$

Thus, $y = (1.185)\ (0.354) + 0.321 = 0.74$

Converting back to proportions $p = [\sin(0.74)]^2 = 0.455$

Following the same procedure for the seedlings-to-adult 1 and seedlings-to-'death' transitions, the p values obtained were 0.030 and 0.524, respectively. These three values sum 1.009. Once standardized to sum to unity, the calculated hypothetical transition probabilities were:

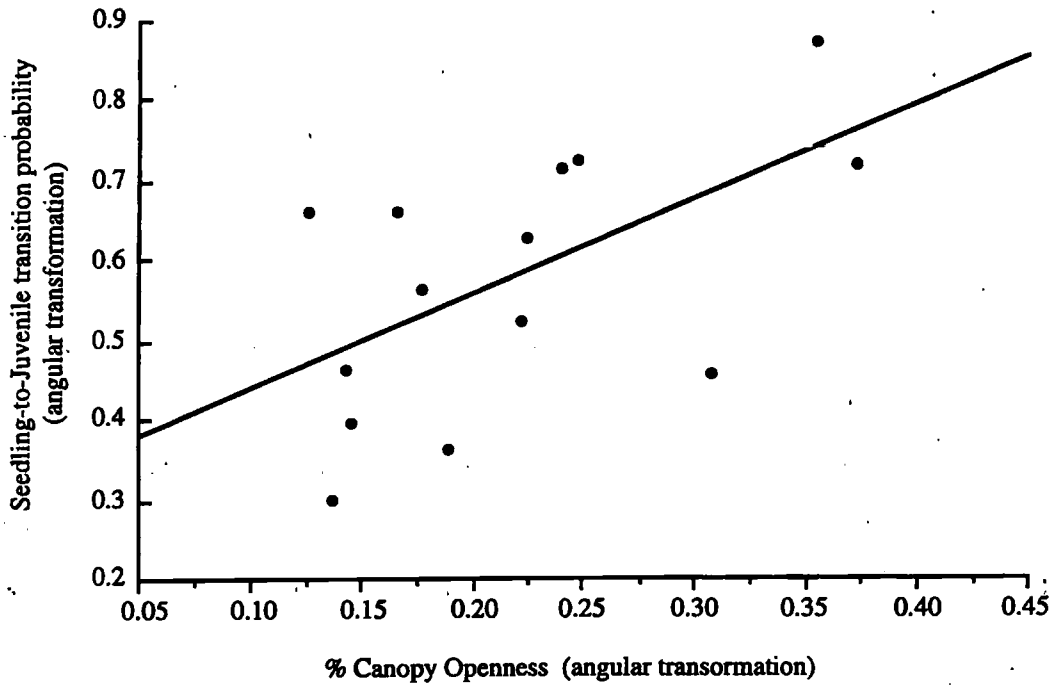
Seedling to juveniles: 0.451

Seedlings to adult 1: 0.030

Seedlings to 'death': 0.519

All matrix entries for each of the four hypothetical projection matrices were calculated in this way, using the parameters of the functions describing the relationship between each entry and light conditions given in Table C.1.

Figure C.1 Relationship between seedling-to-juvenile transition probabilities and diffuse light (both variables angular transformed, q = arcsin ($\sqrt{p}$)), given by y = 1.185 (x) + 0.321.



The resulting hypothetical projection matrices are given in Table C.2. Note that in type-4 matrix the calculated fecundity entries are negative. To obtain the λ value of this matrix these entries were assumed to be zero, except for the fecundity of adults 3, which was given a value of 0.00001 in order for the matrix to attain equilibrium.

Table C.1. Results of the linear regressions performed between each transition probability and light conditions, both variables angular transformed for linearity (except in the case of fecundity entries). Matrix entries are referred to as S - J, i.e. Seedling-to-Juvenile transition. S = seedling, J = juvenile, A1 = adult 1, A2 = adult 2, A3 = adult 3, D = death, m = slope, b = y intercept, R^2 = % of the variance accounted for, p = probability value.

Transition Probability	S - J	S - A1	S - D	J - J	J - A1	J - A2	J - D
m	1.18	-0.51	-0.64	0.58	-0.21	-0.58	0.44
b	0.32	0.35	1.04	0.48	0.71	0.32	0.33
R^2	0.33	0.05	0.06	0.19	0.01	0.05	0.02
p	0.03	0.49	0.040	0.12	0.71	0.45	0.61

Transition Probability	A1 - J	A1 - A1	A1 - A2	A1 - A3	A1 - D	A2 - J	A2 - A1
m	0.22	0.52	-0.18	-1.18	-0.01	0.22	0.49
b	0.18	0.67	0.62	0.41	0.26	0.02	0.28
R^2	0.02	0.13	0.01	0.32	0.00	0.05	0.07
p	0.55	0.20	0.76	0.03	0.99	0.45	0.36

Transition Probability	A2 - A2	A2 - A3	A2 - D	A3 - A1	A3 - A2	A3 - A3	A3 - D
m	0.36	-0.99	-0.05	-0.07	1.14	-1.24	-0.10
b	0.84	0.64	0.12	0.15	0.37	1.17	0.12
R^2	0.09	0.21	0.00	0.00	0.41	0.33	0.01
p	0.29	0.09	0.87	0.90	0.01	0.03	0.75

Fecundity entry	A1 - S	A2 - S	A3 - S
m	0.18	1.0	2.11
b	-0.36	-2.52	-5.09
R^2	0.28	0.38	0.40
p	0.05	0.02	0.01

Table C.2 Calculated patch-specific projection matrices, λ values, and stage-specific mortalities (Qx) for four hypothetical populations under 12%, 6%, 3% and 1.5% canopy openness. Negative fecundities were considered to be zero (or almost zero) in order to calculate the λ value of type-4 matrix (see text).

Stage at time t

	S	J	A1	A2	A3
Type-1 patch			λ = 1.552		
S	0	0	1.775	9.435	20.262
J	0.451	0.498	0.067	0.010	0
A1	0.030	0.446	0.577	0.193	0.017
A2	0	0.017	0.289	0.699	0.510
A3	0	0	0.001	0.086	0.465
Qx	0.519	0.039	0.067	0.010	0.008
Type-2 patch			λ = 1.345		
S	0	0	0.707	3.453	7.584
J	0.341	0.425	0.058	0.006	0
A1	0.053	0.473	0.541	0.155	0.019
A2	0	0.039	0.318	0.670	0.378
A3	0	0	0.013	0.157	0.593
Qx	0.607	0.062	0.069	0.012	0.010
Type-3 patch			λ = 1.101		
S	0	0	0.173	0.462	1.245
J	0.264	0.372	0.051	0.004	0
A1	0.072	0.488	0.504	0.129	0.020
A2	0	0.059	0.333	0.64	0.293
A3	0	0	0.042	0.214	0.675
Qx	0.664	0.081	0.070	0.012	0.011
Type-4 patch			λ = 0.979		
S	0	0	(-0.094)	(-1.033)	(-1.924)
J	0.212	0.336	0.046	0.002	0
A1	0.087	0.495	0.473	0.112	0.021
A2	0	0.075	0.341	0.617	0.238
A3	0	0	0.071	0.256	0.728
Qx	0.701	0.094	0.07	0.013	0.013

In order to build the patch-specific projection matrices reported in Chapter 5, I decided to use the field data available instead of these calculated projection matrices for the following reasons:

1) The relationship between most matrix entries and light conditions is poorly described by a linear function. In Fig. C.1 the linear regression between the seedling-to-juvenile transition and light conditions showed a particularly high R^2 (0.33, which is statistically significant at p=0.03). However, most R^2 values were well below 0.20, which indicates that the data does not distribute linearly along the range of light conditions sampled. Similar results were found when a second degree polynomial, an exponential or a logarithmic curve were fitted to the data. Thus, no simple relationship exists between some matrix entries and percentage canopy openness.

2) Transition probabilities are correlated. Therefore, if a particular matrix entry is calculated through a linear function that does not reflect its variation along the light gradient considered, this would also result in the miscalculation of other matrix entries, even if they are closely described by a linear function.

3) As shown in Chapter 3, population dynamics vary from year to year. Population growth rate was smaller in 1993-94 than in 1992-93 for all populations. By calculating standardize hypothetical matrices based on the empirical data for the two periods studied, I am ignoring this yearly variation that reflects population dynamics in 'good' and 'bad' years (perhaps as a result of the weather conditions). Instead, the hypothetical matrices obtained would describe an intermediate behaviour that would obscure important temporal differences. This could have been partially overcome by calculating two sets of hypothetical matrices based on the empirical data of the two periods separately. However, each matrix entry would have been based on a relationship given by only half the number of data points, with the consequent loss in accuracy.

4) The R^2 of fecundity entries against light conditions were amongst the highest observed, which would suggest that the calculated fecundities were realistic. A linear fit resulted in higher R^2 values than a second order polynomial, a logarithmic or an exponential fit in all cases. Using the obtained linear relationship the fecundity entries of type-4 matrix were negative. From a biological point of view, this would mean that fecundity is zero under a certain level of light conditions. This does not happen in natural populations; positive fecundities were recorded even in populations in the darkest patches sampled (see Chapter 3), despite them showing negative growth rates. Even if fecundities were assumed to be zero in type-4 matrix (except for adult 3 fecundity, that was given a value of 0.00001), the λ value obtained was very close to unity, which suggests that mortality was underestimated. In fact, the R^2 of all mortality transitions against light conditions were very low (Table C.1) and the stage-specific mortalities reported in Table C.2 might be totally unrealistic. As noted in 2), this may automatically lead to inaccuracies in the calculation of other matrix elements.

Appendix C.2

An example of Matrix M, representing spatial heterogeneity, using the 1992-93 data set.
Plant stages are S=seedlings, J=juveniles, A1=small adults, A2=medium adults and A3=large adults.

		Type-1 Patch					Type-2 Patch					Type-3 Patch					Type-4 Patch				
		S	J	A1	A2	A3	S	J	A1	A2	A3	S	J	A1	A2	A3	S	J	A1	A2	A3
	S	0	0	4.469	22.900	44.900	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Type-1	J	0.588	0.423	0.025	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Patch	A1	0.020	0.454	0.562	0.120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A2	0	0.021	0.375	0.780	0.630	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A3	0	0	0	0.100	0.330	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	S	0	0	0	0	0	0	0	0.930	2.196	7.984	0	0	0	0	0	0	0	0	0	0
Type-2	J	0	0	0	0	0	0.440	0.301	0.036	0.004	0	0	0	0	0	0	0	0	0	0	0
Patch	A1	0	0	0	0	0	0.120	0.506	0.504	0.222	0	0	0	0	0	0	0	0	0	0	0
	A2	0	0	0	0	0	0	0.096	0.370	0.631	0.400	0	0	0	0	0	0	0	0	0	0
	A3	0	0	0	0	0	0	0	0.045	0.129	0.580	0	0	0	0	0	0	0	0	0	0
	S	0	0	0	0	0	0	0	0	0	0	0	0	0.011	0.087	0.240	0	0	0	0	0
Type-3	J	0	0	0	0	0	0	0	0	0	0	0.333	0.286	0.024	0	0	0	0	0	0	0
Patch	A1	0	0	0	0	0	0	0	0	0	0	0.100	0.536	0.380	0.049	0.027	0	0	0	0	0
	A2	0	0	0	0	0	0	0	0	0	0	0	0.143	0.503	0.595	0.197	0	0	0	0	0
	A3	0	0	0	0	0	0	0	0	0	0	0	0	0.067	0.347	0.769	0	0	0	0	0
	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.210	0.383	0.825
Type-4	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.333	0.333	0.005	0.007	0
Patch	A1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.286	0.540	0.420	0.128	0.009
	A2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.079	0.378	0.540	0.238
	A3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.016	0.154	0.317	0.733

Appendix C.3

An example of matrix R, which includes the effect of the forest regeneration cycle, for 1992-93 with k=1%
Overall population growth rate = 1.407. Symbols as in Appendix C.2

		Type-1 Patch					Type-2 Patch					Type-3 Patch					Type-4 Patch				
		S	J	A1	A2	A3	S	J	A1	A2	A3	S	J	A1	A2	A3	S	J	A1	A2	A3
	S	0	0	3.084	15.801	30.981	0	0	0	0	0	0	0	0	0	0	0	0	0.045	0.229	0.449
Type-1	J	0.406	0.292	0.017	0	0	0	0	0	0	0	0	0	0	0	0	0.006	0.004	3E-04	0	0
Patch	A1	0.014	0.313	0.388	0.0828	0	0	0	0	0	0	0	0	0	0	0	2E-04	0.005	0.006	0.001	0
	A2	0	0.014	0.259	0.5382	0.435	0	0	0	0	0	0	0	0	0	0	0	2E-04	0.004	0.008	0.006
	A3	0	0	0	0.069	0.228	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0.003
	S	0	0	0.288	0.6808	2.475	0	0	0.642	1.515	5.509	0	0	0	0	0	0	0	0	0	0
Type-2	J	0.136	0.093	0.011	0.0012	0	0.304	0.208	0.025	0.003	0	0	0	0	0	0	0	0	0	0	0
Patch	A1	0.037	0.157	0.156	0.0688	0	0.083	0.349	0.348	0.153	0	0	0	0	0	0	0	0	0	0	0
	A2	0	0.030	0.115	0.1956	0.124	0	0.066	0.255	0.435	0.276	0	0	0	0	0	0	0	0	0	0
	A3	0	0	0.014	0.040	0.180	0	0	0.031	0.089	0.400	0	0	0	0	0	0	0	0	0	0
	S	0	0	0	0	0	0	0	0.003	0.027	0.074	0	0	0.008	0.060	0.166	0	0	0	0	0
Type-3	J	0	0	0	0	0	0.103	0.089	0.007	0	0	0.230	0.197	0.017	0	0	0	0	0	0	0
Patch	A1	0	0	0	0	0	0.031	0.166	0.118	0.015	0.008	0.069	0.370	0.262	0.034	0.019	0	0	0	0	0
	A2	0	0	0	0	0	0	0.044	0.156	0.184	0.061	0	0.099	0.347	0.411	0.136	0	0	0	0	0
	A3	0	0	0	0	0	0	0	0.021	0.108	0.238	0	0	0.046	0.239	0.531	0	0	0	0	0
	S	0	0	0	0	0	0	0	0	0	0	0	0	0.065	0.119	0.256	0	0	0.208	0.379	0.817
Type-4	J	0	0	0	0	0	0	0	0	0	0	0.103	0.103	0.002	0.002	0	0.330	0.330	0.005	0.007	0
Patch	A1	0	0	0	0	0	0	0	0	0	0	0.089	0.167	0.130	0.040	0.003	0.283	0.535	0.416	0.127	0.009
	A2	0	0	0	0	0	0	0	0	0	0	0	0.024	0.117	0.167	0.074	0	0.078	0.374	0.535	0.236
	A3	0	0	0	0	0	0	0	0	0	0	0	0.005	0.048	0.098	0.227	0	0.016	0.152	0.314	0.726

Appendix C.4

An example of matrix D, including the effect of net seed dispersal among patches, for 1992-93, with k=1% and fd=0.2
Symbols as in Appendix C.2.

		Type-1 Patch					Type-2 Patch					Type-3 Patch					Type-4 Patch				
		S	J	A1	A2	A3	S	J	A1	A2	A3	S	J	A1	A2	A3	S	J	A1	A2	A3
	S	0	0	-0.616	-3.158	-6.191	0	0	1E-04	3E-04	9E-04	0	0	1E-06	1E-05	3E-05	0	0	-0.008	-0.044	-0.085
Type-1	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Patch	A1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	S	0	0	-0.057	-0.133	-0.490	0	0	-0.128	-0.303	-1.101	0	0	1E-06	1E-05	3E-05	0	0	0.001	0.002	0.004
Type-2	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Patch	A1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	S	0	0	0.001	0.003	0.005	0	0	-0.001	-0.005	-0.014	0	0	-0.002	-0.012	-0.033	0	0	0.001	0.002	0.004
Type-3	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Patch	A1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	S	0	0	0.016	0.084	0.164	0	0	0.003	0.008	0.029	0	0	-0.013	-0.023	-0.050	0	0	-0.007	-0.013	-0.027
Type-4	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Patch	A1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix C.5

An example of matrix E, integrating the forest regeneration cycle and seed dispersal, for 1992-93, with k=1% and fd=0.2.
Overall population growth rate = 1.354. Symbols as in Appendix C.2.

		Type-1 Patch					Type-2 Patch					Type-3 Patch					Type-4 Patch				
		S	J	A1	A2	A3	S	J	A1	A2	A3	S	J	A1	A2	A3	S	J	A1	A2	A3
	S	0	0	2.467	12.643	24.790	0	0	1E-04	3E-04	9E-04	0	0	1E-06	1E-05	3E-05	0	0	0.037	0.185	0.364
Type-1	J	0.406	0.292	0.017	0	0	0	0	0	0	0	0	0	0	0	0	0.006	0.004	3E-04	0	0
Patch	A1	0.014	0.313	0.388	0.083	0	0	0	0	0	0	0	0	0	0	0	2E-04	0.005	0.006	0.001	0
	A2	0	0.014	0.259	0.538	0.435	0	0	0	0	0	0	0	0	0	0	0	2E-04	0.004	0.008	0.006
	A3	0	0	0	0.069	0.228	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0.003
	S	0	0	0.231	0.547	1.985	0	0	0.513	1.212	4.408	0	0	1E-06	1E-05	3E-05	0	0	0.001	0.002	0.004
Type-2	J	0.136	0.093	0.011	0.001	0	0.304	0.208	0.025	0.003	0	0	0	0	0	0	0	0	0	0	0
Patch	A1	0.037	0.157	0.156	0.069	0	0.083	0.349	0.348	0.153	0	0	0	0	0	0	0	0	0	0	0
	A2	0	0.030	0.115	0.196	0.124	0	0.066	0.255	0.435	0.276	0	0	0	0	0	0	0	0	0	0
	A3	0	0	0.014	0.040	0.180	0	0	0.031	0.089	0.400	0	0	0	0	0	0	0	0	0	0
	S	0	0	5E-04	0.003	0.005	0	0	0.003	0.022	0.060	0	0	0.006	0.048	0.133	0	0	0.001	0.002	0.004
Type-3	J	0	0	0	0	0	0.103	0.089	0.007	0	0	0.230	0.197	0.017	0	0	0	0	0	0	0
Patch	A1	0	0	0	0	0	0.031	0.166	0.118	0.015	0.008	0.069	0.370	0.262	0.034	0.019	0	0	0	0	0
	A2	0	0	0	0	0	0	0.044	0.156	0.184	0.061	0	0.099	0.347	0.411	0.136	0	0	0	0	0
	A3	0	0	0	0	0	0	0	0.021	0.108	0.238	0	0	0.046	0.239	0.531	0	0	0	0	0
	S	0	0	0.016	0.084	0.164	0	0	0.003	0.008	0.029	0	0	0.052	0.095	0.205	0	0	0.201	0.367	0.790
Type-4	J	0	0	0	0	0	0	0	0	0	0	0.103	0.103	0.002	0.002	0	0.330	0.330	0.005	0.007	0
Patch	A1	0	0	0	0	0	0	0	0	0	0	0.089	0.167	0.130	0.040	0.003	0.283	0.535	0.416	0.127	0.009
	A2	0	0	0	0	0	0	0	0	0	0	0	0.024	0.117	0.167	0.074	0	0.078	0.374	0.535	0.236
	A3	0	0	0	0	0	0	0	0	0	0	0	0.005	0.048	0.098	0.227	0	0.016	0.152	0.314	0.726